Organic farming and generalist predator communities: Implications for conservation biological control in agroecosystem

vom Fachbereich Biologie der Technischen Universität Darmstadt

zur

Erlangung des akademischen Grades

eines Doctor rerum naturalium

genehmigte

Dissertation von

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Tag der Einreichung: 11.04.2007

Tag der mündlichen Prüfung: 11.05.2007

Darmstadt 2007

D17

Allmendfeld, May 2006

Beer Sheva, December 2005

The most exciting phrase to hear in science, the one that heralds the most discoveries, is not "Eureka!" (I found it!) but "That's funny..."

Isaac Asimov

PEER-REVIEWED PUBLICATIONS IN THIS THESIS

Chapter 2
Birkhofer K, Bezemer TM, Bloem J, Bonkowski M, Christensen S, Ekelund F, Fließbach A, Hedlund K, Mikola J, Robin C, Mäder P, Setälä H, Tatin-Froux F, van der Putten WH and Scheu S (2007) Long-Term organic farming fosters below- and aboveground biota: Implications for internal nutrient cycling and biological control. (submitted)

Chapter 3
Birkhofer K, Fließbach A, Wise DH, Scheu S (2007) Generalist predators in long-term organically and conventionally managed grass-clover fields in Switzerland: Implications for conservation biological control. (submitted)

Chapter 4
Birkhofer K, Scheu S, Wise DH (2007) Small scale spatial pattern of web-building spiders (Araneae) in alfalfa: Relationship to prey availability, disturbance from cutting and intraguild interactions. Environmental Entomology (accepted)

Chapter 5
Birkhofer K, Wise DH, Scheu S (2007) Effects of prey from the detrital food web and habitat complexity on generalist predator numbers and herbivore suppression. (submitted)

Chapter 6
Birkhofer K, Gavish E, Endlweber K, Lubin YD, von Berg K, Wise DH and Scheu S (2007) Cursorial spiders retard aphid population growth at low densities in a winter wheat field in central Germany. (in preparation)

FURTHER PEER-REVIEWED PUBLICATIONS

Vučić-Pestić O, Birkhofer K, Scheu S, Brose U (2007) Habitat structure, predator interference and prey aggregation determine the functional response of a soil predator-prey interaction. Oikos (accepted)

Haubert D, Birkhofer K, Fließbach A, Gehre M, Scheu S, Ruess L (2006) Stable isotope analysis in fatty acids to investigate a soil food web. (submitted)

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Zusammenfassung

Bewirtschaftungsmaßnahmen im organischen Landbau fördern Nährstoffkreisläufe und die Bodenqualität. In der vorliegenden Studie wird die Wirkung von organischer und konventioneller Bewirtschaftung auf generalistische Prädatoren in einem agrarökologischen Langzeitversuch (DOK Versuch, Schweiz) untersucht und verfahrensabhängige Faktoren analysiert.

Viele der untersuchten Tiergruppen, die in der biologischen Schädlingskontrolle einsetzbar sind und zudem interne Nährstoffkreisläufe unterstützen, wurden durch organische Bewirtschaftung in Weizenfeldern gefördert. Die Verwendung von anorganischen Düngern hingegen wirkte sich negativ auf zahlreiche nützliche Tiergruppen aus. Spinnen (Araneae) wurden besonders durch organischen Landbau gefördert, was in den untersuchten Weizenfeldern wahrscheinlich auf größerer Beuteverfügbarkeit basierte. Auch in einem zweiten untersuchten Agrarökosystem (Kleegraswiesen) reagierten Spinnen, als einzige generalistische Prädatoren, positiv auf organische Düngung. Im Gegensatz zum Weizen zeigten hier aber nur die laufaktiven Spinnen eine erhöhte Aktivitätsdichte. Die Unterschiede zwischen organisch und konventionell bewirtschafteten Flächen waren früh und spät in der Anbausaison am größten.

Der Einfluss der Beuteverfügbarkeit und der Vegetationsstruktur auf generalistische Prädatoren wurde in einem Freilandexperiment genauer untersucht. Eine Erhöhung der strukturellen Komplexität zwischen Weizenständen wirkte sich negativ auf die Aktivitätsdichten von laufaktiven Spinnen und Laufkäfern (Carabidae) aus. Im Gegensatz dazu führte die Erhöhung der Beuteverfügbarkeit von Zersetzern (Collembola) zu höheren Aktivitätsdichten von netzbauenden Spinnen und Kurzflügelkäfern (Staphylinidae). Mit zunehmender Aktivitätsdichte von Zersetzerbeute nahm die Blattlausdichte (Aphididae) zu. Diese positiven Beute-Beute Interaktionen können die Schädlingskontrolle durch generalistische Prädatoren verringern, da der Fraß an Schädlingen durch das Auftreten von alternativer Beute reduziert werden kann. Die Ergebnisse der vorliegenden Studie machen deutlich, dass weitere Untersuchung zum Einfluss von Vegetationsstruktur und Beuteverfügbarkeit auf die natürliche Schädlingskontrolle nötig sind.

Natürliche Schädlingskontrolle wird durch Kannibalismus, intragilde Prädation und Konkurrenz zwischen generalistischen Prädatoren beeinflusst. Durch Analyse der räumlichen Verteilung von

netzbauenden Spinnen in Luzernefeldern wurde nachgewiesen, dass Konkurrenz oder Abstoßung durch Artgenossen zu einer regelmäßigen Verteilung von Spinnennetzen beiträgt. Blattläuse waren bei hohen Dichten aggregiert, eine räumliche Verteilung die von Spinnen nicht gezeigt wurde. In allen Untersuchungen zeigten Spinnen die stärkste und einheitlichste Antwort auf organische Bewirtschaftung, wobei die räumliche Analyse auf intragilde Interaktionen zwischen Spinnen hinweist. Daher wurde in einem weiteren Freilandexperiment die Auswirkung funktioneller Gruppenidentität auf Blattlauspopulationen im Weizen untersucht. Nur die laufaktiven Spinnen verlangsamten das anfängliche Populationswachstum von Blattläusen. Diese Ergebnisse werden durch molekularbiologische Untersuchungen weiter gestützt, da ein hoher Anteil der laufaktiven Spinnen positiv auf Blattlaus DNA getestet wurde.

Organische Bewirtschaftung verändert die Pflanzen- und Tiergemeinschaft auf Äckern und damit die Aktivität, Dichte und räumliche Verteilung von generalistische Prädatoren. Die vorliegende Arbeit zeigt, dass generalistische Prädatoren (insbesondere laufaktive Spinnen) durch organischen Landbau gefördert werden und zur Optimierung der natürlichen Schädlingsbekämpfung beitragen können. Der Zusammenhang zwischen Bewirtschaftungsmaßnahmen und Habitatveränderungen sollte in weiteren Studien vertieft untersucht werden, um in Zukunft Bewirtschaftungsstrategien zu entwickeln die gezielt generalistische Prädatoren fördern und zu einer Optimierung der natürlichen Schädlingskontrolle beitragen.

Summary

Organic farming systems rely on improved soil quality and biological control favored by reduced tillage and pesticide application, organic fertilizer application and crop rotation management. The first part of this study focused on the impact of organic and conventional long-term farming (DOK Trial, Switzerland), primarily characterized by fertilizer types, on major aboveground generalist predator taxa (spiders, rove beetles and ground beetles) in structurally simple (winter wheat) and complex (grass-clover) agroecosystem.

Most analyzed animal taxa that improve internal nutrient cycling and biological control in agroecosystems benefited from organic farming and several taxa were negatively affected by inorganic fertilizer or herbicides application. Spiders (Araneae) benefited most from organic farming in wheat fields. Conventionally managed wheat fields had higher plant coverage, the positive numerical response of spiders therefore most likely was a consequence of enhanced availability of non-pest prey in organically managed fields. Similar to results from wheat fields, spiders were more active and diverse in organically managed grass-clover fields. In contrast to wheat fields, only surface-active spiders responded positive, with strongest responses early and late in the season. As in wheat fields spider activity-density and plant cover did not correlate early in the season, suggesting that spider activity-density and prey availability were correlated early in the season.

Prey availability and vegetation structure caused a numerical response of spiders in organically managed fields; both factors were further analyzed in a field experiment in wheat. Increasing the structural complexity between wheat stands reduced the activity-density of cursorial spiders and ground beetles (Carabidae). Web-building spiders and rove beetles (Staphylinidae) responded positively to experimentally enhanced availability of alternative non-pest prey (Collembola), but cursorial spiders and ground beetles did not mirror prey responses. Aphid numbers increased with increasing activity-density of alternative prey. Such positive prey-prey relationship potentially reduces pest suppression by generalist predators, as non-pest prey may distract predators from aphid prey. Organic farming practices may enhance spider activity, abundance and diversity via changes in plant community composition and prey availability. Nevertheless structurally richer, weedier fields and enhanced density of soil biota in organic farming systems may reduce pest suppression.

The role of generalist predators as biological control agents is affected by cannibalism, intraguild predation and competition between predators. Spatial patterns of web-building spiders in alfalfa did not resemble the aggregation of available pest prey (aphids). In contrast web-owners had fewer neighbors in the vicinity of their webs than expected under a random distribution of spider webs in times of highest spider activity. Spiders were most affected by organic management in the DOK trial and experiments in grass-clover and alfalfa suggest strong intraguild interactions at high densities. To evaluate the consequences of functional group identity for pest suppression, two major spider functional groups (web-builders and cursorial spiders) were manipulated in a cage experiment in wheat. Cursorial spiders slowed down the initial aphid population growth, but none of the treatments prevented an aphid outbreak. Molecular studies strengthen this result, as they indicate that cursorial species had the highest proportion of individuals that tested positive for aphid DNA.

Results of this study suggest that cursorial spiders may be of particular importance as natural enemies under organic farming. They responded most consistent to organic farming across agroecosystems with different structural complexity and successfully slowed down aphid population growth during early colonization stages. Future studies need to analyze the factors responsible for the reaction of generalist predators to farming methods. Results may further identify conditions under which enhanced predator numbers result in improved pest suppression.

Chapter 1 - General Introduction

1.1. AIMS AND SCOPE

This study analyzes the impact of long-term organic farming on generalist predator communities as compared to conventionally managed agroecosystems. In addition to this applied objective, mechanisms that cause a response by generalist predators to farming systems are analyzed in field experiments. Results contribute to the understanding of predator responses to characteristics of organically managed arable land and may help optimizing conservation biological control in different farming systems.

1.2. ORGANIC FARMING

The term organic farming dates back prior to 1940 when it defined management practices that improve soil fertility through the application of animal wastes (Heckman 2006). Today organic management refers to strategies focused on avoiding the use of synthetic fertilizers and pesticides to minimize environmental damage. These systems therefore represent an ecosystem-oriented approach to agricultural production that ideally motivates farmers to reduce the negative environmental impact of agriculture (Häni et al. 1998). A long-term study by Mäder et al. (2002) in Switzerland suggests that the financial income under organic farming is comparable to conventional farming, while associated pollution levels and soil degradation are reduced. Yields were on average 20% lower in organically managed crops, but costs for synthetic pesticides and inorganic fertilizers in conventional farming negated this advantage. The only comparable multidisciplinary study did not report a difference in vegetable yields comparing organic and conventional tomato farming systems (Drinkwater et al. 1995). Indications of economic feasibility correlate with increasing consumer awareness as the public favours environmentally sound agricultural production (Tilman et al. 2002). The world-wide market for certified organic food is therefore continuously growing at considerably higher rates than for conventionally produced agricultural products (Willer and Yussefi 2005).

1.3. FARMING SYSTEM COMPARISON

Farming practices affect most below- and aboveground animal groups. The pattern of reduced biodiversity in modern agricultural areas has been attributed to detrimental local farming practices and landscape changes (Bengtsson et al. 2005, Hole et al. 2005, Poschlod et al. 2005). Local on farm practices affect ecosystem processes such as nutrient cycling and biological control (Dick 1992, Zehnder et al. 2007). Several studies analyzed farming system effects on animal communities with most of those comparisons (i) focusing on single taxa, (ii) comparing the fauna of farms in different areas or (iii) dealing with short-term or transitional effects of organic farming (but see Mäder et al. 2002).

The first type of study provides valuable information about farming system effects on distinct groups, but does not indicate the consequences for associated ecosystem services, as interactions between different animal groups affect most processes (e.g. biological control or decomposition). Farming system comparisons of spatially separated farms only provide conclusive information if they incorporate details about differences in local soil types, farming system history and landscape composition (e.g. Schmidt et al. 2005). Several studies suggest that soil properties change slowly under transition from conventional to organic farming and may require several years or even decades to reach equilibrium (Clark et al. 1998, Fließbach et al. 2007). Therefore, it is crucial to study the impact of organic farming in agroecosystems with a long-term farming system history (Raupp et al. 2006).

1.4. EFFECTS ON GENERALIST PREDATORS

Generalist predators are primarily carnivorous species with a relatively wide prey spectrum (for definition see Symondson et al. 2002). Three taxa are among the most abundant aboveground generalist predator groups in European agroecosystems: Araneae, Carabidae and Staphylinidae.

1.4.1. Araneae

Spiders are abundant generalist predators in most agroecosystems (Riechert and Lockley 1984) with a strictly carnivorous diet. Two functional groups can be distinguished regarding the way prey is

captured: (1) species that use silk to construct webs and (2) species that hunt prey actively. Functional groups can roughly be defined on family level (Uetz et al. 1999), but several exceptions have been identified on species level (Thornhill 1983, Alderweireldt 1994b, Harwood et al. 2005).

The spider fauna of temperate European agroecosystems is well described and is dominated by members of two families (Nyffeler and Sunderland 2003). Sheet-web weavers (Linyphiidae) either rely on web captured prey or sometimes also hunt for prey (Alderweireldt 1994b) and wolf spiders (Lycosidae) which solely forage actively (Samu et al. 2003). Most agrobiont spider species disperse through aerial drifting by climbing to exposed parts of the vegetation and then using silk strands to get drifted by wind (ballooning, Weyman et al. 2002). This passive dispersal improves the ability of spiders to recolonize agroecosystem after human disturbance (e.g. harvest or tillage).

1.4.2. Coleoptera, Carabidae

Carabid beetles are a less homogeneous generalist predator group in terms of feeding and dispersal behavior. Several species mainly feed on live animal prey, but scavenging, seed or fungi feeding species are also abundant in agroecosystems (Toft and Bilde 2002). Dispersal range in carabids is limited as not all species are able to fly (Holland 2002). The carabid fauna of temperate agroecosystems is well described, being dominated by few carnivorous and omnivorous species (Kromp 1999, Purtauf et al. 2005).

1.4.3. Coleoptera, Staphylinidae

Staphylinid beetle communities in agroecosystems are less well studied than spiders and carabids (but see Krooss and Schaefer 1998, Elliott et al. 2006). Several species feed on fungi, whereas many are carnivorous or parasitic (Clough et al. 2007). Most small species are good flyers and are able to colonize arable fields from overwintering sites outside of arable fields (Markgraf and Basedow 2002). The relatively small size of some dominant species (Aleocharinae), the less strictly carnivorous diet and the high mobility presumably contributed to the scarcity of studies compared to other generalist predator taxa in European agroecosystems.

1.5. DOK TRIAL

The DOK trial in Therwil, Switzerland, is an agricultural long-term experiment that offers a unique possibility to study long-term effects of farming systems under well defined soil and landscape conditions. The experiment was established in 1978 by the Agroscope Reckenholz-Tänikon research station (ART) and the Research Institute of Organic Agriculture (FiBL) to compare different farming systems and their impact on below- and aboveground processes. The experiment originally consisted of two organic farming systems (BIODYN, BIOORG), one conventional (CONFYM) system, an unfertilized control and another control plot series receiving only the conventional pesticides. In 1985 the latter was converted to a second conventional system mimicking stockless farming (CONMIN) by only applying mineral fertilizers and pesticides. The second conventional system (CONFYM) also receives farmyard manure in addition to mineral fertilizers according to the guidelines for integrated farming in Switzerland (for details see Table 1.1.).

Table 1.1. Farming systems established in the DOK agricultural long-term trial in Therwil, Switzerland. Major farming system differences are given through the different fertilizer types and plant protection measures.

	Bio-dynamic	Bio-organic	Conventional	Conventional (stockless)
	BIODYN	BIOORG	CONFYM	CONMIN
farmyard manure	composted & slurry	rotted & slurry	stacked	-
inorganic fertilizer	-	-	NPK	NPK
weed control	mechanical		mechanical & herbicides	
disease control	indirect methods		chemical (threshold)	
insect control	plant extracts		chemical (threshold)	
special treatments	biodynamic preparations	-	plant growth regulators	

Each farming system is replicated on four 10 x 20 m plots with three different crops per year and managed in a standardized crop rotation system (Figure 1.1.). Plots are arranged in a Latin square design and split in two halves (5 x 20 m) with one half receiving moderate (0.7 livestock units) and the other half receiving moderate quantities (1.4 livestock units) of treatment specific fertilizer. Crop rotation and soil tillage regimes are identical and synthetic insecticides are only applied infrequently to conventional systems based on threshold decisions.

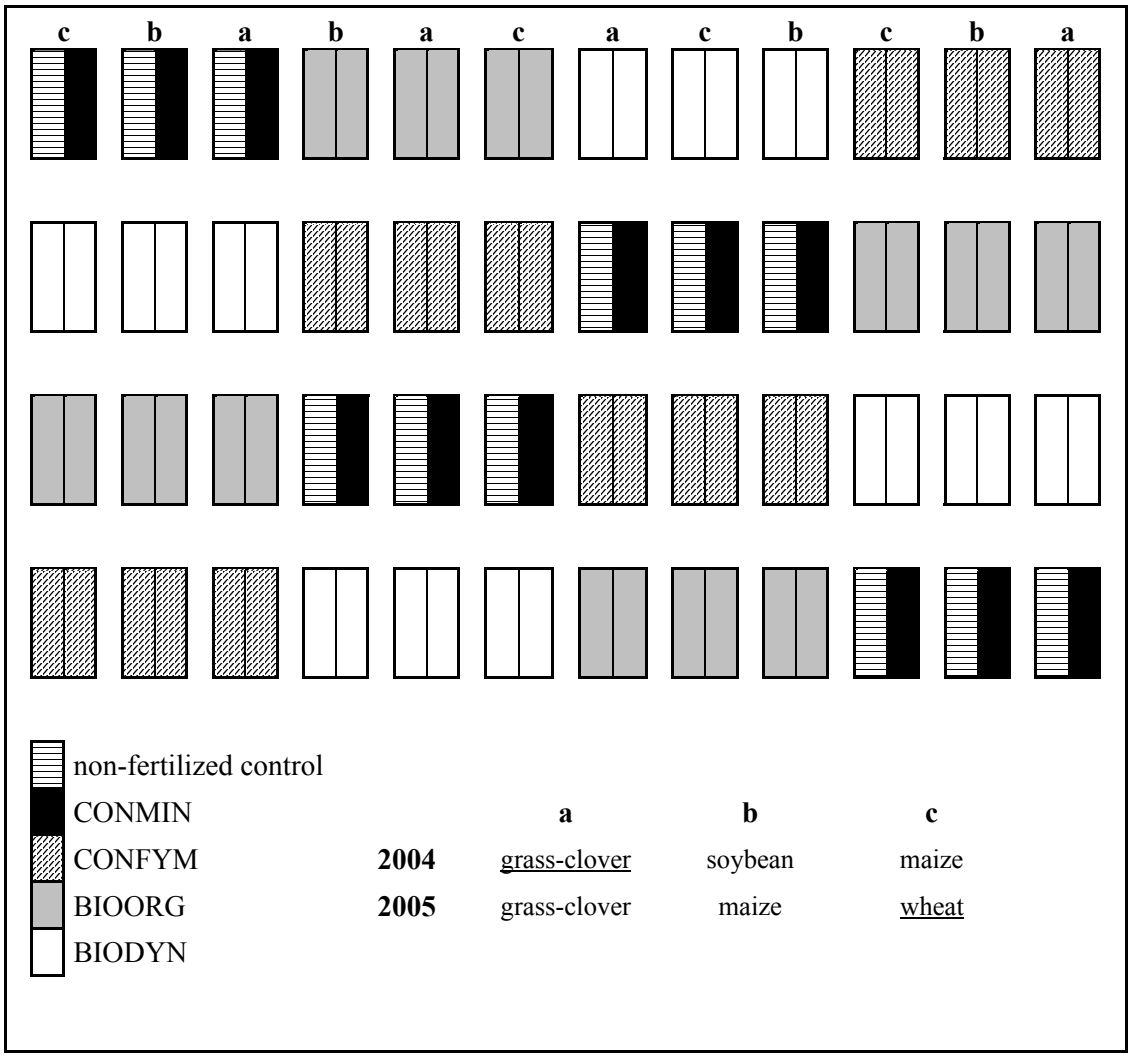

Figure 1.1. Map of the DOK trial with different patterns indicating the farming system and small letters indicating different crops. Note that each 10 x 20 m large main plot is split in two halves, with one half receiving low (0.7 livestock units ha^{-1}) and the other half receiving moderate (1.4 livestock units ha^{-1}) quantities of treatment specific fertilizer. Sampled crops in 2004 and 2005 are underlined.

1.6. MANAGEMENT IMPACT

Several studies suggest a negative impact of certain farming systems on generalist predator abundance and diversity. Traditionally the majority of those studies focused on the consequences of insecticide application (e.g. Wang et al. 2001, Thomas and Jepson 1997) and mechanical management practices (e.g. Holland and Reynolds 2003, Thorbek and Bilde 2004). The farming systems established in the DOK trial are managed with identical tillage regimes and decisions about insecticide applications in the conventional systems are based on restrictive thresholds. The specific farming systems mainly differ in the type of fertilizer used and the weed management strategy (Table 1.1.).

Side-effects of herbicide application on animal taxa are primarily indirect, with weak or no direct lethal effects on spiders (Baines et al. 1998, Haughton et al. 2001), ground beetles (Brust 1990, Taylor 2006) and rove beetles (Samsøe-Petersen 1995, Sterk et al. 1999). Most authors report delayed indirect effects on generalist predators that only occurred several months after herbicide application (but see Bell et al. 2002b). This negative impact is attributed to habitat changes as herbicides reduce plant diversity and structural complexity in agroecosystems.

Carabid abundance and diversity is enhanced by nutrient enrichment through sewage sludge or urea-phosphate fertilizer as compared to unmanaged sites (Larsen et al. 1996), similar results are documented for Staphylinidae (Krooss and Schaefer 1998). This effect is again attributed to improved plant growth under fertilization and the associated favorable microclimate. There is increasing evidence that organic matter addition also enhances the abundance of decomposer taxa (Pimentel and Warneke 1989, Moreby et al. 1994, Eaton et al. 2004) and most generalist predators potentially utilize prey from the decomposer subsystem in addition to herbivore prey ("dual subsystem omnivory", Scheu 2001). Any indirect positive effect of fertilization on generalist predators can therefore not solely be ascribed to vegetation characteristics, an assumption that still requires experimental verification.

1.7. BIOLOGICAL CONTROL

Improving habitat conditions for specific animal functional groups in agroecosystems remains economically insignificant if the involved species do not provide an important ecosystem service. Generalist predator communities in agroecosystems contribute to herbivore suppression thereby preventing pest outbreaks and reducing yield loss due to herbivore damage (Symondson et al. 2002). Barbosa (1998) defined conservation biological control as pest suppression through an already established natural enemy community. With the increasing importance of organic farming and the reduced public acceptance of pesticide use, measures that strengthen the natural control of pest populations have recently received considerable attention (Zehnder et al. 2007).

Criticism about the use of generalist predators as biological control agents focuses on intraguild interactions. Intraguild predation as "the killing and eating of other species that use the same resources

and are therefore potential exploitative competitors" (Polis 1988) is common among generalist predators and may reduce pest control (Rosenheim et al. 1995). Cannibalism further affects generalist predator populations and may reduce herbivore suppression (Wise 2006). Indeed, recent field experiments indicate negative effects of generalist predator interactions on pest control (Snyder and Ives 2001, Prasad and Snyder 2006).

1.8. HYPOTHESES

The present research was conducted to identify consequences of long-term organic farming on generalist predators and to identify factors responsible for the observed differences. Subsequently, the role of enhanced predator abundance for biological control was analyzed. The following specific hypotheses are tested and discussed in individual chapters:

CHAPTER 2 "Long-term organic farming fosters below- and aboveground biota: Implications for internal nutrient cycling and biological control"

The long-term addition of organic matter and the avoidance of herbicide application improve nutrient cycling and biological control due to strengthening beneficial components of the microbial and animal community in structurally simple agroecosystems (winter wheat).

CHAPTER 3 "Generalist predators in long-term organically and conventionally managed grass-clover fields in Switzerland: Implications for conservation biological control"

The long-term addition of organic matter strengthens generalist predator populations and improves biological control in frequently cut and structurally complex agroecosystems (grass-clover).

CHAPTER 4 "Small scale spatial pattern of web-building spiders (Araneae) in alfalfa: Relationship to prey availability, disturbance from cutting and intraguild interactions"

Web-building spiders aggregate in response to the distribution of available pest prey, with no impact of intraguild interactions or cutting on pattern development in alfalfa agroecosystems.

CHAPTER 5 "Effects of prey from the detrital food web and habitat complexity on generalist predator numbers and herbivore suppression"

Alternative non-pest prey and increased habitat complexity cause a positive numerical response of generalist predators and enhance pest suppression in wheat fields.

CHAPTER 6 "Cursorial spiders retard aphid population growth at low densities in a winter wheat field in central Germany"

Spiders significantly reduce aphid population growth in wheat, independent of functional group identity or diversity.

Fig. 2.1. DOK trial Therwil, Switzerland

Chapter 2 - Long-term organic farming fosters below- and aboveground biota: implications for internal nutrient cycling and biological control

2.1. ABSTRACT

Organic farming is considered as a sustainable alternative for conventional agriculture. Inorganic fertilizer use and pesticide application significantly affect soil organic matter, soil fertility and above- and belowground species. We investigated in a comprehensive way soil chemical, as well as below- and aboveground biological parameters of two organic (bioorganic and biodynamic) and two conventional farming systems (with and without livestock) in wheat fields within a long-term agricultural experiment (DOK trial, Switzerland). Soil carbon content was significantly increased in systems receiving farmyard manure and concomitantly microbial biomass (fungi and bacteria) was enhanced. Microbial activity parameters, such as microbial basal respiration and nitrogen mineralization, showed an opposite pattern, suggesting that soil carbon in the conventional system was more easily accessible to microorganisms than in organic systems. Bacterivorous nematodes and earthworms both were most abundant in the organic systems, which is in line with the responses of their potential food sources (microbes and organic matter). However, the neutral lipid fatty acid biomarker for mycorrhizal fungi, and the density of Protozoa, Chilopoda and Collembola did not differ between the farming systems. Mineral fertilizer application detrimentally affected enchytraeids and Diptera larvae, whereas aphids as important pests benefited. Spider abundance was favored by organic management, most likely a response to increased weed diversity and density. The two-fold higher abundance of this generalist predator group in organic systems likely contributed to the significantly lower aphid abundance. In conclusion, long-term organic farming enhanced microbial activities in the soil, some of their predators and ecosystem engineering by earthworms, suggesting enhanced nutrient cycling. Conventional systems based on farmyard manure were in between organic systems and systems based on mineral fertilizer. Mineral fertilizers and weed/pest control reduced the potential for

top-down control of aboveground pests, however, conventional farming systems differed more from organic systems in their belowground than in aboveground attributes. The conventional system mimicking stockless farming had the lowest organic matter content with negative consequences for several microbial and soil animal groups. Our results strongly suggest that organic farming improves internal nutrient cycling and pest control, and therefore allows managing arable systems in a sustainable way.

2.2. INTRODUCTION

A main goal of organic farming is to reduce environmental damage with minimum effect on economic profit (Bengtsson et al. 2005). Two key management decisions in farming systems concern the use of organic *vs*. mineral fertilizer and to reduce, or stop, the application of pesticides for crop protection. Little is known about the integral consequences of organic farming on communities of soil organisms, which drive nutrient cycling in agroecosystems. Even fewer studies analyzed both below- and aboveground biota. A number of current studies compare organic and conventional farming practices at a landscape scale (Bengtsson et al. 2005, Fuller et al. 2005), however, these comparisons as well may include historical contingency effects and differences in soil abiotic conditions. Therefore, to analyze effects of organic *vs.* conventional farming systems on nutrient cycling, as well as aboveground invertebrate pests and potential antagonists long-term agroecological experiments are necessary.

Agroecosystems are highly productive systems with open nutrient cycles. They loose nutrients through runoff, leaching, denitrification, removal of crop residues and harvest and consequently depend on continuous nutrient inputs to compensate for nutrients losses (Tivy 1987). Long-term application of organic fertilizer may result in an increase in the carbon content of soils (Drinkwater et al. 1995, Fließbach et al. 2007) and in the promotion of bacteria and fungi (McLaughlin and Mineau 1995), as microbes and especially fungi are often resource limited in arable land (Wardle 2002). This, in turn, affects decomposition of crop residues and hence the availability of nutrients (Doran et al. 1998, Lundquist et al. 1999). Allochthonous resource input by organic fertilization further influences the soil fauna (Bünemann et al. 2006). In fact, effects of increased carbon availability may cascade up

to higher trophic levels; Halaj and Wise (2002) for example documented that fungivorous and predatory taxa benefited from detrital subsidies. Surface active predators, in turn, may benefit from increased prey availability, which could lead to enhanced efficiency of biological control of pests in agroecosystems (Scheu 2001). Fertilization can also be detrimental to soil biota, e.g. high rates of slurry application may reduce the availability of oxygen (Andres 1999). Effects of organic fertilizers are usually strong in arable soils low in organic matter, e.g. due to removal of plant biomass (Tivy 1987).

NPK fertilizer application may reduce soil organic matter levels as compared to farmyard manure application (Ryan 1999). On the other hand, mineral fertilization may also increase soil organic matter levels due to enhanced plant growth and residue returns. Reduced organic carbon levels may limit bacterial and fungal growth, and this may propagate into higher trophic levels of the soil food web. Moreover, application of mineral fertilizer may negatively affect soil microarthropods, e.g. due to salt stress, or changes in soil acidity (Bulluck et al. 2002). Furthermore, mineral fertilizer application decreases the root-to-shoot ratio of plants. As a result, the extension of the rhizosphere is reduced with potential implications for below- and aboveground herbivores (Andrzejewska 1976).

Pesticide application in conventionally managed systems affects below- and aboveground animal communities, with the effects varying with animal taxa and the chemical components used. Effects of herbicide (isoproturon) application on below- and aboveground animals may be weak, only a single omnivorous nematode species out of 24 tested species was harmfully affected (Sterk et al. 1999). This is in line with other studies documenting weak direct effects of herbicide application on below- and aboveground animals (Bell et al. 2002b, Lindsay and French 2004, Pereira et al. 2005, Bünemann et al. 2006). In contrast, indirect effects on animal communities, mediated via plant community changes, are well documented (Wardle et al. 1993, Taylor et al. 2006).

Most studies on microbial and animal communities in agroecosystems focus on their role in decomposition processes and nutrient cycling (De Ruiter et al. 1993, 1994); however, usually only single or few community components are analyzed (for reviews see Bengtsson et al. 2005, Hole et al. 2005). Considering the increased attention that sustainable farming practices receive, the lack of knowledge on how different farming systems and their specific management practices influence

below- and aboveground community structure is unfortunate. Since sustainable management practices essentially rely on the fostering of internal nutrient cycling, knowledge on soil organisms as drivers of nutrient mineralization is indispensable (Hendrix et al. 1986, Didden et al. 1994).

This study investigates effects of four farming systems on soil processes and biota, including soil chemistry, microorganisms, soil fauna and aboveground fauna of winter wheat fields in a long-term agricultural experiment (DOK trial, Switzerland; Mäder et al., 2002). The design of the experiment allowed evaluating farming system differences between (i) conventional and organic farming, (ii) stockless farming and mixed farming, (iii) conventional farming with livestock and organic farming, (iv) stockless conventional farming and mixed farming and between (v) organic farming with composted and with rotted farmyard manure. We expect positive effects of farmyard manure on internal nutrient cycling and pest resilience. We further hypothesize that organic farming will primarily increase the biomass and activity of microbial soil communities with limited consequences for below- and aboveground animal diversity and abundance.

2.3. METHODS

Study site and experimental design

The DOK trial (bio**D**ynamic, bio**O**rganic, **K**onventionell) in Therwil, Switzerland is a long-term agricultural experiment established in 1978 by the Agroscope Reckenholz-Tänikon research station (ART) and the Research Institute of Organic Agriculture (FiBL) to analyze organic and conventional farming practices and their impact on soil and aboveground processes. The soil is a haplic luvisol on deep deposits of alluvial loess. Mean precipitation is 785 mm per year with an annual average temperature of 9.5°C (Mäder et al. 2002).

We analyzed wheat plots of two organic farming systems (BIODYN, BIOORG), one conventional (CONFYM) system, receiving farm yard manure, and a second conventional system mimicking stockless farming (CONMIN, receiving mineral fertilizers only; see Table 2.1.).

Table 2.1. Farming systems established in the DOK trial in Therwil, Switzerland. Terms and abbreviations given in this table are used throughout the text. Fertilizer (farmyard manure = FYM, inorganic = NPK) and mean annual nutrient amendments between 1978 and 2005 to all systems during four crop rotation periods. Table modified from Fließbach et al. (2007).

Treatment name	Biodynamic	Bioorganic	Conventional	Mineral
Abbreviation	BIODYN	BIOORG	CONFYM	CONMIN
Organic fertilizer	Composted FYM,	Rotted FYM,	Stacked FYM,	-
Inorganic fertilizer	-	-	NPK	NPK
Weed control	Mechanical		Mechanical & chemical	
Disease control	Indirect methods		Chemical (threshold)	
Pest control	Plant extracts		Chemical (threshold)	
Special treatments	Biodynamic	-	Plant growth regulators	
Nutrients (kg ha^{-1} yr^{-1})				
$C_{organic}$	1818	2272	2272	0
N_{total}	99	102	157	122
$N_{mineral}$	31	35	101	122
P	23	27	41	40
K	165	157	258	250

Note that the conventional systems are farmed according to Integrated Plant Production Standards (IPP).

Crop rotation, comprising of cereal crops, root crops and grass-clover, and soil tillage regime were identical for all 5x20 m^2 large plots. Synthetic insecticides were last applied to potatoes in 2001 in the conventional systems CONFYM and CONMIN, and soils of these systems were also treated with a molluscicide (Limax plus with metaldehyde as active ingredient) in 2003 (soybeans) and 2004 (maize). A single herbicide containing the active ingredients carfentrazone and isoproturon was applied to winter wheat in both conventional systems on 1st April 2005 and the growth regulator trinexapac-ethyl was applied on 22nd April 2005. The two conventional systems received a total of 90 kg N ha^{-1} as calcium ammonium nitrate in March and April 2005, BIOORG received a total of 44 m^3 slurry ha^{-1} in two rates (N_{tot} 77.9, N_{min} 33.2, organic matter 1335 kg ha^{-1}) and BIODYN 30 m^3 ha^{-1} (N_{tot} 46.2, N_{min} 28.5, organic matter 651 kg ha^{-1}) only once.

Soil sampling

All four replicated wheat plots of each farming system were sampled on 9 May 2005 by collecting seven small soil cores (diameter 8 cm, depth 5 cm), one large soil core (diameter 20 cm, depth 5 cm) and one sample of bulk soil (1 kg) from the upper 5 cm layer of randomly chosen locations at the

northern and southern end of each of the plots (minimum edge distance 1.5 m). Bulk soil was used to analyze chemical soil properties and microbial parameters; soil cores or homogenized soil from soil cores (Nematodes) were used to analyze soil fauna.

Soil chemistry

Soil pH was measured in 0.1 M KCl solution in a soil to liquid ratio of 1:3 (w/v). Total soil nitrogen and carbon were measured using an elemental analyzer (Carlo Erba, Milan, Italy) and were taken to represent total soil nitrogen content (N_{tot}) and soil organic carbon content (C_{org}), as concentrations of carbonates are generally low at the study site. To measure soil water content fresh soil samples were dried at 105°C for 72 h.

Microorganisms

To measure soil microbial biomass soil samples were sieved (2 mm mesh) and the water content was adjusted to 40–50% maximum water holding capacity. One week before analysis, soil samples were pre-incubated at 20ºC. Soil microbial biomass C (C_{mic}) and N (N_{mic}) was measured by chloroform-fumigation-extraction (CFE) according to Vance et al. (1987; for details see Fließbach et al. 2007). The C_{mic}-to-C_{org} ratio was calculated from data on microbial biomass carbon and soil carbon content.

The abundance of bacteria and fungi was estimated using direct counting and phospholipid fatty acid (PLFA) analysis. Direct microscopic counts of bacteria and fungi were performed on soil smears (Bloem and Vos 2004). Slides for bacterial counts were analyzed following Bloem et al. (1995). Bacterial biomass carbon was estimated from the biovolume using a carbon content of 3.1×10^{-13} g C μm^{-3}. Slides for fungal counts were stained with differential fluorescent stain, a mixture of europium chelate (stains nucleic acids red) and fluorescent brightener (stains polysaccharides in cell walls blue). Unstained fungal hyphae visible with transmitted light were included in the counts. Total hyphal length was measured using the grid intersection method and an epifluorescence microscope at 400x magnification. Biovolume was calculated using the equation $V = (\pi/4)W^2(L-W/3)$, where W = width

(μm) and L = length (μm). Fungal biomass was calculated assuming a mean hyphal diameter of 2.5 μm and a specific carbon content of $1.3x10^{-13}$ g C μm^{-3}.

Lipid extractions for analysis of PLFAs and NLFAs were made on 3 g of fresh soil according to Frostegård et al. (1993) and Hedlund (2002). The resulting fatty acid methyl esters were separated on a Hewlett Packard 6890 gas chromatograph. Relative retention times of the fatty acid methyl esters were compared to those of standards. The sum of the PLFAs i15:0, a15:0, 15:0, i16:0, 16:1ω9, i17:0, a17:0, cy17:0, 18:1ω7, and cy19:0 was used as an index of bacterial biomass (Frostegård and Bååth 1996). The amount of PLFA 18:2ω6 was used as an index of non-mycorrhizal fungal biomass and NLFA 16:1ω5 as a marker for arbuscular mycorrhizal fungi (Olson 1999, Hedlund 2002).

Microbial basal respiration (Anderson and Domsch 1978) was measured using an automated respirometer system based on electrolytic O_2-microcompensation (Scheu 1992). Samples were pre-incubated for one week at 20°C and 40–50% of their maximum water holding capacity and subsequently analyzed. For basal respiration, the average O_2 consumption rate (μl O_2 g^{-1} h^{-1}) of samples not amended with glucose during hours 10-20 after attachment to the respirometer system was used. The specific respiration (qO_2; μl O_2 mg^{-1} C_{mic} h^{-1}) was calculated from data on microbial biomass (C_{mic}) and basal respiration.

Microbial activity of the different soils was estimated by indices calculated from the capacity of the microbial biomass to utilize ^{14}C glucose added to the soil (for details see Nguyen and Henry 2002). The microbial growth parameter A describes the fraction of the added ^{14}C that is mineralized during the rapid mineralization phase. The microbial maintenance parameter C represents the fraction of added ^{14}C that was mineralized at the end of the slow mineralization phase.

Potential nitrogen mineralization rate in soil was determined by incubating soil samples at 20ºC and 50% water holding capacity for six weeks (Bloem et al. 1994). N mineralization rate was calculated from the increase in mineral N concentration between week six and week two, excluding data from week one to reduce any effect of sample handling.

Soil fauna

The abundance of heterotrophic flagellates and naked amoebae was estimated using the most probable number method (Rønn et al. 1995). Samples of soil (about 1 g fresh wt) from each replicate plot were mixed with 20 ml of 'Modified Neff's amoeba saline' (Page 1988) and subsequently blended for one minute in a Waring Laboratory Blender (7012S) at 22,000 RPM. A three-fold dilution series in Costar (3598) microtiter plates (8 replicates of 12 dilutions) was then amended with 100 µl of Tryptic Soy Broth (0.1 g l^{-1}; Difco Bacto, Detroit, Michigan, USA). The plates were stored in darkness at 10°C and analyzed for the presence of protozoa after one and three weeks incubation using an Olympus inverted microscope (IMT-2). Data on protozoan presence/absence were transformed to protozoan most probable numbers using specific software (F. Ekelund and R. Rønn, pers. comm.).

Nematodes were extracted from 120 g subsamples of soil using Oostenbrink elutriators (Oostenbrink 1960), killed by heat and fixed (35% formaldehyde diluted to 4%). The total number of nematodes was counted and a minimum of 150 nematodes were further identified to family or genus level according to Bongers (1988) and allocated to feeding groups according to Yeates et al. (1993).

Enchytraeids were extracted from soil using a combination of cold and hot wet funnel extraction methods to maximize the extraction efficiency. A soil sample was first submerged in cold water for 24 h in a plastic sieve following the protocol in Dunger and Fiedler (1997), and later heated for 3-4 h in a wet funnel following the protocol of O'Connor (1955). The individuals were identified to species or genus level. Other soil animals were extracted from one large (20 cm diameter; macrofauna) and one small soil core (5 cm diameter; mesofauna) using a modified heat extraction system (Kempson et al. 1963). Samples were stored in ethanol for later identification.

Aboveground fauna

The vegetation-based fauna was sampled on May 16 under dry conditions using an Eco-Vac insect suction sampler (EcoTech, Bonn, Germany). An area of 0.7 m² was fenced on each of the two sides of each plot (PVC barriers, 50 cm high) and immediately suction sampled for 90 s. Samples were transferred to glass vessels containing a small amount of ethyl acetate. Suction samples were stored at -10°C and later sieved and hand sorted using a dissecting microscope (Leica MZ12) to separate

animals from debris. To estimate densities of surface active animals an area of 2.0 m² was fenced (PVC barriers; 50 cm high, 10 cm sunk into the soil) and four pitfall traps containing a water detergent mix were placed along the inner barrier and left open for 14 days (May 3 to 17). Pitfall samples were transferred to 70% ethanol, sieved and later hand sorted. On May 9 vegetation coverage of each plot was estimated by two independent visual inspections of ground covered by plants.

Species diversity

To analyze effects of different farming regimes on the biodiversity of below- and aboveground fauna, species richness, Shannon-Wiener diversity index and evenness index were calculated for nematodes, enchytraeids, spiders and carabids in each plot.

Statistical analysis

All variables were log transformed to achieve homogeneity of variance and subsequently analyzed by planned comparisons, using five predefined contrasts:

(a) CONFYM & CONMIN versus BIOORG & BIODYN (conventional *vs.* organic farming)

(b) CONMIN versus CONFYM, BIOORG & BIODYN (conventional stockless *vs.* mixed farming)

(c) CONFYM versus BIOORG & BIODYN (conventional with livestock *vs.* organic farming)

(d) CONMIN versus CONFYM (conventional stockless *vs.* conventional with livestock)

(e) BIOORG versus BIODYN (organic farming with composted *vs.* rotted FYM)

Data are only presented in figures for variables that significantly differed ($P < 0.05$) for at least one contrast. We further assigned each variable to one of five categories (soil chemistry, microbial biomass, microbial activity, soil fauna, and aboveground fauna). The variables of each category were ordinated by principal components analysis (PCA) using CANOCO (ter Braak and Smilauer 2002). The sample scores of the four PCA axes were further analyzed for individual categories (fixed factor MANOVA) and subsequently treatment effects on categories were analyzed by planned comparisons using predefined contrasts as described above. Vegetation coverage data were angular transformed; differences between conventional (CONFYM & CONMIN) and organic managed systems (BIOORG & BIODYN) were inspected by contrast analyses.

2.4. RESULTS

Soil chemistry

Soil pH ranged from 4.5 to 5.8 in different farming systems; it was lowest in the CONMIN system being 0.7 pH units lower than in the CONFYM system (Fig. 2.1.a).

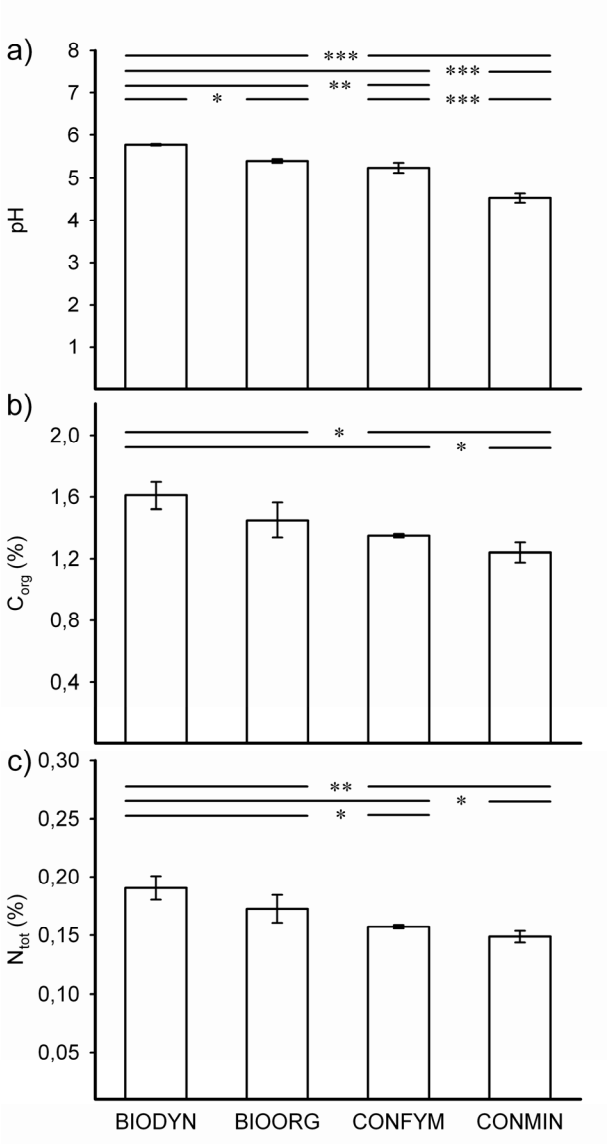

Figure 2.1. Arithmetic mean of (a) Soil pH, (b) organic carbon content (C_{org}), (c) and total nitrogen content (N_{tot}), the latter two expressed in % of the soil dry mass in different farming systems. BIODYN = organic farming with composted manure, BIOORG = organic farming with rotted manure, CONFYM = conventional farming with manure, CONMIN = stockless conventional farming. Significant differences are indicated by contrast analysis; *= $P < 0.05$;**= $P < 0.01$;***= $P < 0.001$. Error bars indicate standard errors.

CONFYM and the two organic systems (BIOORG & BIODYN) differed significantly albeit the differences were relatively minor. The BIODYN soils had the highest pH and this was the only

difference between BIOORG and BIODYN. Soil organic carbon (C_{org}) and total soil nitrogen (N_{tot}) were lowest in the CONMIN and highest in the BIODYN system (Fig. 2.1.b-c). Soil carbon content increased by 9% from CONMIN to CONFYM, by 8% from CONFYM to BIOORG and by 11% from BIOORG to BIODYN. Soil carbon-to-nitrogen ratio did not differ significantly between any of the systems averaging 8.5. Also, soil moisture did not significantly differ between farming systems and was on average 24% of dry weight at the time of sampling.

Microbial biomass

Microbial biomass parameters increased in the order CONMIN < CONFYM < BIOORG ≤ BIODYN (Fig. 2.2.a-f).

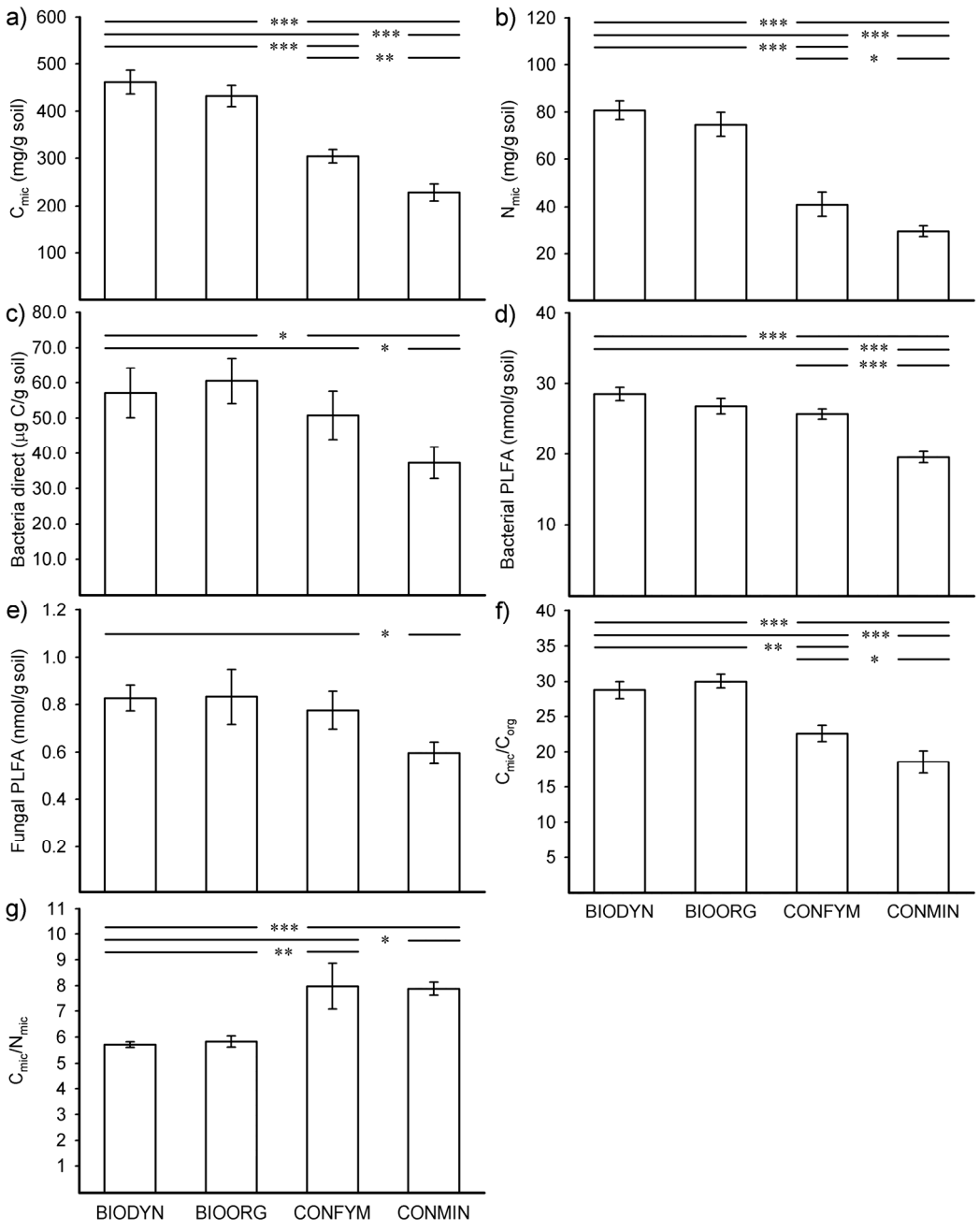

Figure 2.2. Arithmetic mean of (a) Microbial biomass carbon (C_{mic}), (b) microbial biomass nitrogen (N_{mic}), (c) bacterial biomass (bacteria direct, fluorescence microscopy), (d) bacterial marker PLFA, (e) fungal marker PLFA, microbial biomass carbon to organic carbon ratio (f) and (g) microbial biomass carbon to microbial biomass nitrogen ratio in different farming systems. For legend see Fig 2.1.

C_{mic} and N_{mic} significantly separated CONMIN, CONFYM and organic farming systems but not BIOORG and BIODYN (Fig. 2.2.a-b). C_{mic} in BIODYN systems exceeded that in CONMIN systems by more than 2-fold. This difference was even more pronounced for N_{mic}, with a 2.7-fold increase. Bacterial biomass (fluorescence microscopy; Fig. 2.2.c), bacterial PLFAs and the fungal PLFA 18:2ω6 discriminated the CONMIN system from the other farming systems with the CONFYM system being intermediate between the CONMIN and both organic systems (Fig. 2.2.c-e). Bacterial biomass and bacterial PLFA markers were 1.5 times higher in BIODYN as compared to CONMIN; the respective factor for the fungal PLFA 18:2ω6 was 1.4. Hyphal biomass of fungi measured by fluorescence microscopy, including saprotrophic and mycorrhizal fungi, (mean of all farming systems 11.7 μg C g^{-1} dry wt) and the biomarker for mycorrhizal fungi, NLFA 16:1ω5, (4.58 nmol g^{-1} dry wt) did not differ significantly between farming systems.

The C_{mic}-to-C_{org} ratio was similar in BIOORG and BIODYN systems but significantly higher than in CONFYM and CONMIN systems (Fig. 2.2.f). The C_{mic}-to-N_{mic} ratio showed an inverse pattern compared to all other microbial biomass parameters. It was similar in the two conventional systems averaging 7.93, but considerably lower in the two organic systems BIOORG and BIODYN averaging 5.77 (Fig. 2.2.g).

Microbial activity

Microbial basal respiration did not differ significantly between farming systems averaging 2.07 µl O_2 g^{-1} dry wt h^{-1}. Due to the similar basal respiration, microbial specific respiration (qO_2) followed an inverse pattern to microbial biomass carbon and N_{mic} (Fig. 2.3.a).

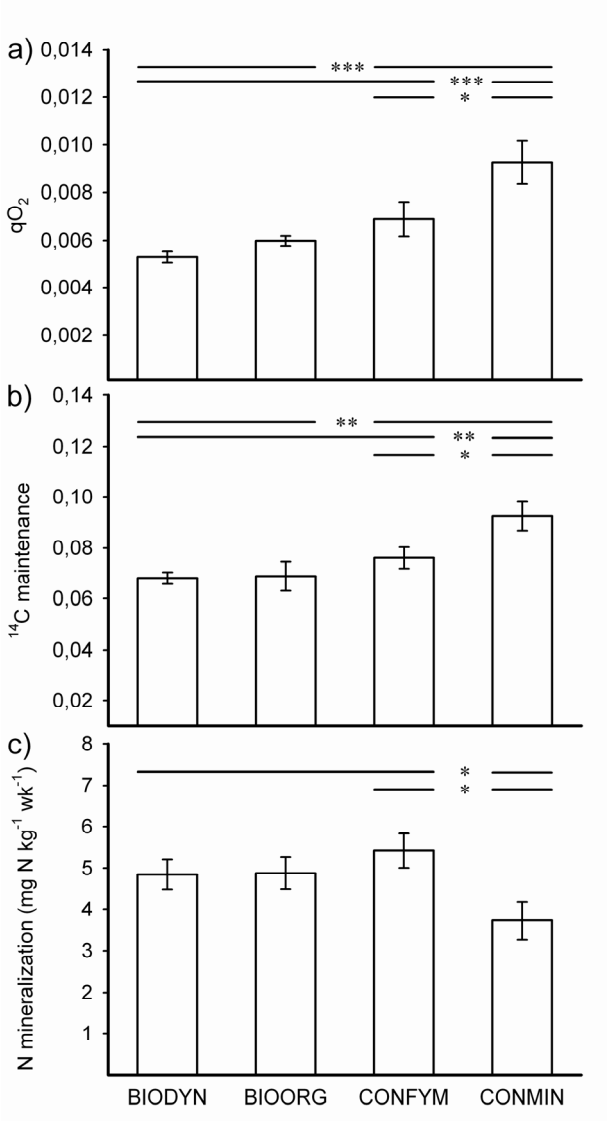

Figure 2.3. Arithmetic mean of (a) Respiratory quotient (qO_2), (b) ^{14}C maintenance parameter and (c) nitrogen mineralization in different farming systems. For legend see Fig 2.1.

In the CONMIN system qO_2 exceeded that in the BIODYN system by a factor of almost two. The ^{14}C maintenance parameter ($C_{maintenance}$; Fig. 2.3.b) in the CONMIN system significantly exceeded that in each of the other farming systems, in particular BIOORG and BIODYN. Nitrogen mineralization was at a minimum in CONMIN and similar in the other three farming systems receiving farmyard manure (Fig. 2.3.c).

Soil fauna

Bacterivorous, herbivorous and omnivorous nematodes were about twice as abundant in BIODYN and BIOORG farming systems than in the CONMIN system, while the opposite was true for fungivorous nematodes (Fig. 2.4.a-d, f).

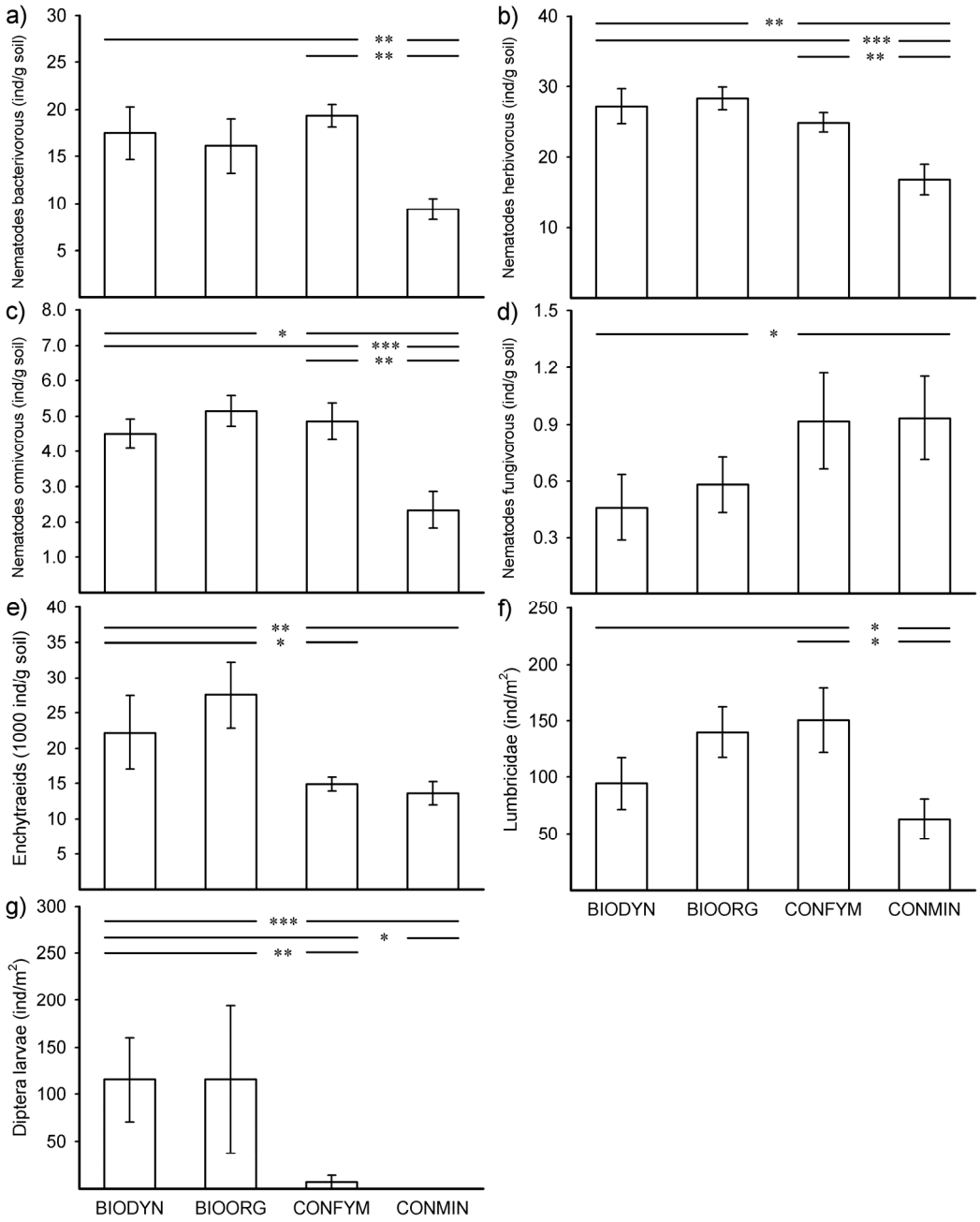

Figure 2.4. Arithmetic mean of the abundance of (a) bacterivorous nematodes, (b) herbivorous nematodes, (c) omnivorous nematodes, (d) fungivorous nematodes, (e) enchytraeids, (f) earthworms and (g) Diptera larvae (Brachycera) in different farming systems. For legend see Fig 2.1.

Enchytraeid abundance was lowest under pesticide and NPK fertilizer application, with nearly twice as high densities in BIOORG and BIODYN systems as compared to CONMIN and CONFYM (Fig. 2.4.e). Earthworm density was at a maximum in farming systems receiving FYM exceeding that in the CONMIN system by a factor of two (Fig. 2.4.f). Fly larvae (Diptera, Brachycera) were almost absent from CONMIN and CONFYM systems, but reached densities of 116 ind m^{-2} in BIODYN and BIOORG systems (Fig. 2.4.g). Abundance of Protozoa (overall mean 156,382 ind. g^{-1} dry wt) and Chilopoda (overall mean 70 ind. m^{-2}) and the generally very low abundance of euedaphic Collembola (1177 ind. m^{-2}), mainly consisting of Isotomidae, did not differ between the farming systems.

Aboveground fauna and vegetation

Adult web-building spiders were more than twice as abundant in BIODYN and BIOORG as in the two conventional systems (Fig. 2.5.a).

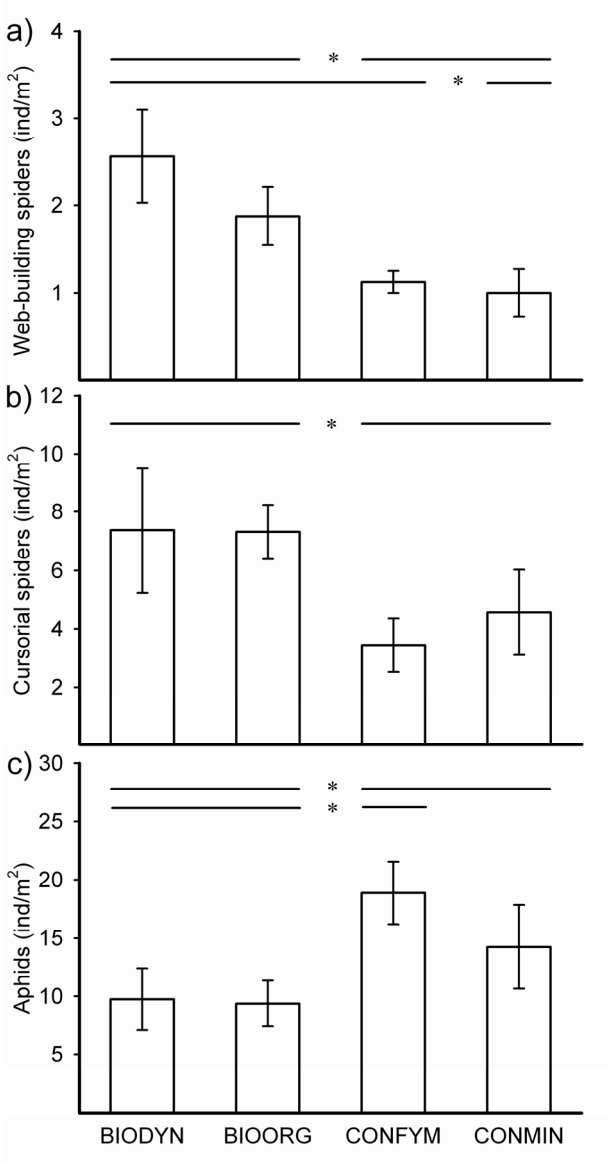

Figure 2.5. Arithmetic mean of the abundance of (a) adult web-building spiders, (b) adult cursorial spiders and (c) aphids in different farming systems. For legend see Fig 2.1.

Similarly, the density of cursorial spiders was up to 1.8 times higher in the two organic systems (Fig. 2.5.b). As typical for the early growth season, numbers of aphids were generally low. Nevertheless, densities in the two conventional farming systems CONMIN and CONFYM exceeded those in the organic systems BIODYN and BIOORG by a factor of 1.7 (Fig. 2.5.c). Aphid abundance was highest in the CONFYM system. Other surface active animals, whether predators (Staphylinidae

33 ind. m^{-2}, Carabidae 18 ind. m^{-2}), herbivores (herbivorous beetles 10 ind. m^{-2}) and decomposers (Entomobryidae 50 ind. m^{-2}), did not respond to farming practices.

Plant cover was significantly higher in the two conventional systems (average cover 89%) than in organic systems (73%; contrast analysis $F_{1,12}$=31.52, P<0.001), although the density of wheat shoots was similar in all systems (sowing distance 16.7 cm).

Diversity of fauna

Nematode species richness tended to be higher in both organic systems as compared to the CONMIN system (contrast analysis $F_{1,12}$=4.03, P=0.068). Neither species richness nor Shannon-Wiener indices differed for other taxa (Enchytraeidae, Araneae and Carabidae).

Ordination

Soil chemistry parameters differed significantly between farming systems (Fig. 2.6.a; MANOVA $F_{12,24}$=6.24, P<0.001) classifying the systems receiving FYM (BIODYN, BIOORG and CONFYM) as significantly different from the stockless conventional system (CONMIN, contrast analysis; Table 2.2.). Further, the two conventional farming systems differed significantly, with the CONFYM system being also significantly different from the two organic systems.

Table 2.2. Contrast comparison based on fixed factor MANOVA results using sample scores of four axes from PCA for each parameter category (a-e). Contrasts were specified to compare different farming systems:
a) CONFYM & CONMIN versus BIOORG & BIODYN (conventional *vs.* organic farming)
b) CONMIN versus CONFYM, BIOORG & BIODYN (stockless farming *vs.* mixed farming)
c) CONFYM versus BIOORG & BIODYN (conventional with livestock *vs.* organic farming)
d) CONMIN versus CONFYM (conventional stockless *vs.* conventional with livestock)
e) BIOORG versus BIODYN (organic farming with rotted *vs.* composted FYM)

	Soil chemistry		Microbial biomass		Microbial activity		Soil fauna		Aboveground fauna	
Contrast	$F_{4,9}$	P	$F_{4,9}$	P	$F_{4,9}$	P	$F_{4,9}$	P	$F_{4,9}$	P
a	28.813	<0.001	20.357	<0.001	5.109	0.019	6.573	0.009	5.340	0.018
b	35.547	<0.001	14.977	<0.001	7.165	0.007	5.452	0.016	1.013	0.450
c	7.245	0.006	7.851	0.005	1.478	0.287	5.548	0.016	5.545	0.016
d	13.980	<0.001	2.472	0.119	3.533	0.054	4.427	0.030	1.218	0.368
e	2.831	0.090	0.513	0.728	0.909	0.498	0.539	0.711	2.591	0.108

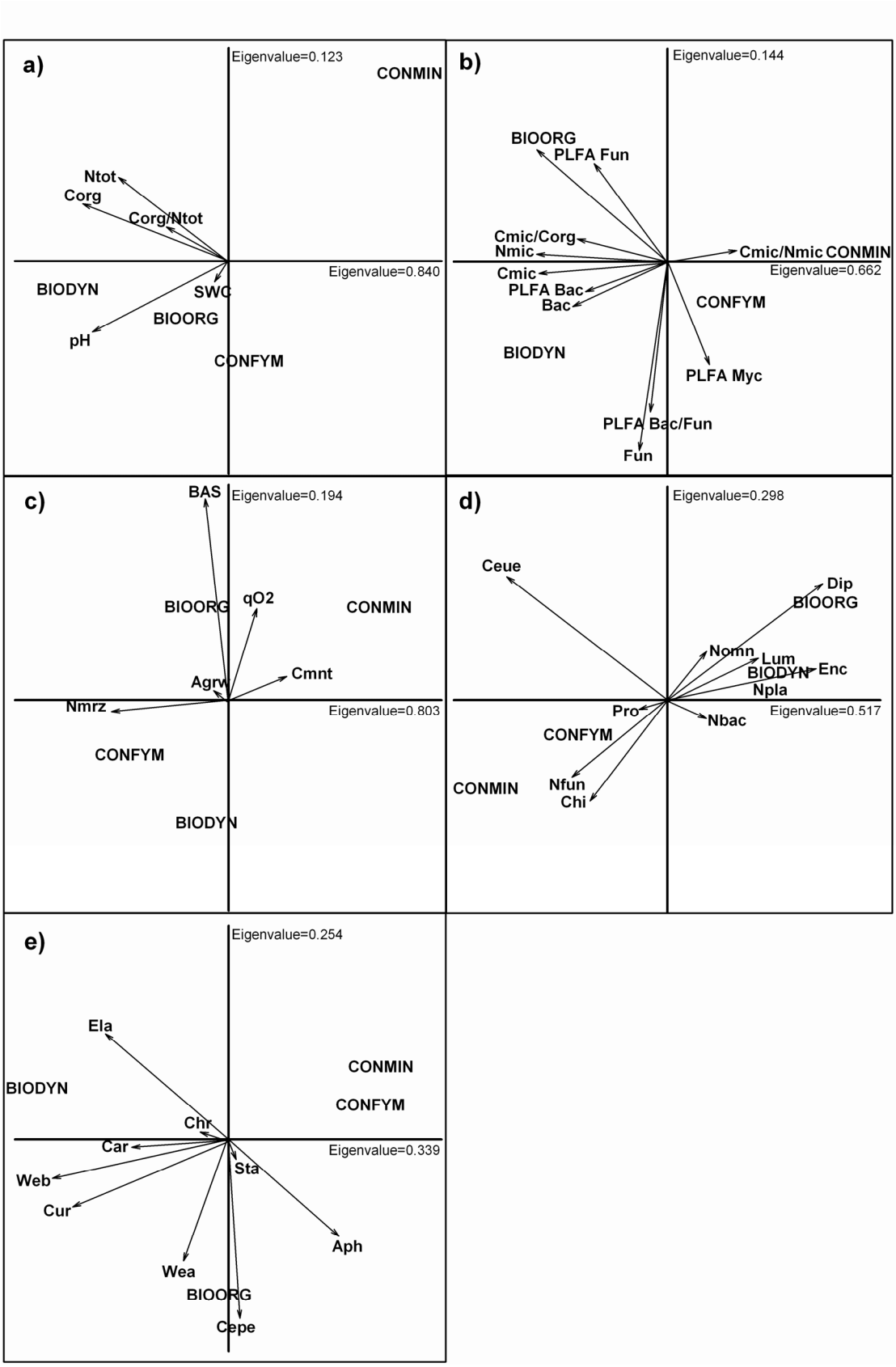

Figure 2.6. Principal components analysis for five parameter categories (a-e), showing sample scores of all analyzed variables per category and treatment positions as centroids (log-transformed data). Treatments see table 2.1.

a) soil chemistry

C_{org} = organic carbon content, C_{org}/N_{tot} = organic carbon to nitrogen ratio, N_{tot} = total nitrogen content, pH = soil pH , SWC = soil water content

b) microbial biomass

Bac = bacterial biomass (fluorescence microscopy), C_{mic} = microbial biomass carbon, C_{mic}/C_{org} = ratio microbial biomass carbon to organic carbon content, C_{mic}/N_{mic} = ratio microbial biomass carbon to microbial biomass nitrogen, Fun = fungal biomass (fluorescence microscopy), $NLFA_{Myc}$ = mycorrhizal marker NLFA, N_{mic} = microbial biomass nitrogen, $PLFA_{Bac/Fun}$ = ratio bacterial PLFA to fungal PLFA, $PLFA_{Bac}$ = bacterial marker PLFA, $PLFA_{Fun}$ = fungal marker PLFA

c) microbial activity

A_{grw} = ^{14}C growth parameter, BAS = basal respiration, C_{mnt} = ^{14}C maintenance parameter, N_{mrz} = nitrogen mineralization, qO_2 = respiratory quotient

d) soil fauna

Dip = Diptera larvae, Chi = Chilopoda, C_{eue} = euedaphic Collembola, Enc = Enchytraeidae, Lum = Lumbricidae, N_{fun} = fungivorous Nematodes, N_{pla} = herbivorous Nematodes, N_{omn} = omnivorous Nematodes, N_{bac} = bacterivorous Nematodes, Pro = Protozoa

e) aboveground fauna

Aph = Aphids, Car = Carabidae, Chr = Chrysomelidae, C_{epe} = epedaphic Collembola, Cur = cursorial spiders, Ela = Elateridae, Sta = Staphylinidae, Wea = Curculionidae (Weavils), Web = web building spiders

Microbial biomass (Fig. 2.6.b; MANOVA $F_{12,24}$=3.46, P=0.005) and microbial activity parameters (Fig. 2.6.c; MANOVA $F_{12,24}$=2.35, P=0.036) also discriminated the organic systems (BIOORG and BIODYN) from the CONMIN system (contrast analysis; Table 2.2.). In contrast to soil chemistry parameters, both microbial biomass and activity did not discriminate the CONFYM from the CONMIN system. Microbial activity parameters also did not separate the CONFYM system from both organic systems.

The soil fauna community significantly differed between farming systems (Fig. 2.6.d; MANOVA $F_{12,24}$=3.32, P=0.006), with a highly significant difference between conventional systems (CONFYM and CONMIN) and organic systems (BIOORG and BIODYN; Table 2.2.). The reaction of the soil fauna to different farming systems mirrored the differences in soil chemical parameters, although generally the response was weaker. Similar to the soil fauna, the aboveground arthropod community differed significantly between conventional managed fields and those receiving organic fertilizers, although the difference was less pronounced (Fig. 2.6.e; MANOVA $F_{12,24}$=2.38, P=0.034). Aboveground fauna was the only analyzed category that did not significantly separate the CONMIN from the other systems.

2.5. DISCUSSION

The farming systems investigated differed markedly in chemical, microbial and faunal properties. The analyzed parameters suggest improved internal nutrient cycling and more efficient pest control in organic systems compared to systems receiving mineral fertilizers and pesticides, in particular to the system receiving only mineral nutrients (CONMIN). In addition to general differences between conventional and organic farming systems, abiotic soil properties and soil fauna composition also separated the two conventional systems.

Soil chemistry

Soil organic carbon (C_{org}) and total soil nitrogen content (N_{tot}) were 18-19% higher in both organic systems than in the conventional systems, whereas there were no significant differences between the two conventional systems. Since one conventional (CONFYM) and both organic systems received equivalent amounts of FYM, the long-term application of additional mineral fertilizer and/or pesticides likely counteracted the build-up of a more humus-rich mineral soil. This observation supports earlier findings that mineral N addition increases the decomposition rate of organic residues by satisfying N requirements of microorganisms (Jenkinson et al. 1985). Fließbach et al. (2007) studied the long-term development of soil organic matter in the DOK trial and found soil organic matter levels to remain relatively stable in the BIODYN system, whereas they were decreasing in all other systems. A lower pH in conventional systems (particularly CONMIN) combined with a significant loss of soil organic carbon might be explained by the use of acidifying mineral fertilizers. NPK fertilizer application could reduce soil particle aggregation and therefore the protection of soil organic matter in microaggregates (Mikha and Rice 2004). This may also apply to the conventional systems in the DOK trial, where aggregate stability is higher in organic systems (Mäder et al. 2002).

Microbial biomass and activity

Similar to soil chemical properties, microbial parameters separated the CONFYM system from both organic systems. Despite receiving similar amounts of organic fertilizer as the BIOORG system, microbial biomass was 30% lower in this system whereas nitrogen mineralization rates were on

average 10% higher. The stockless conventional system CONMIN showed a similar pattern with both C_{mic} and N_{mic} being lower than in organic systems (-49% and -62% compared to the BIOORG and BIODYN systems, respectively), while microbial activity was higher (respiratory quotient +39% and ^{14}C maintenance parameter +26%). This suggests that soil carbon in the CONMIN system is more easily accessible to microorganisms than in both organic systems. In the organic systems, carbon fixed in microbial biomass is increased but higher microbial biomass is associated with reduced losses through respiration (see also Fließbach and Mäder 2000). Presumably, due to the availability of nutrients in excess, the structure of the microbial community in the conventional systems shifted dominance towards early successional species with high turnover rates at the expense of competitive species with more efficient resource use.

The fungal and bacterial PLFA markers were increased by 17-18% in systems receiving FYM as compared to the CONMIN system. Wander et al. (1995) reported no significant difference in the PLFA profile comparing different agricultural management systems, whereas O'Donnell et al. (2001) identified differences between treatments receiving either FYM and inorganic fertilizer or NPK fertilizer only. Results of our study suggest long-term consequences of farming systems for microorganisms with bacteria and fungi increasing in biomass by the addition of organic fertilizers, even if applied in combination with mineral fertilizers and pesticides (CONFYM). PLFA profiles indicate that the increased input of organic matter affects microbial populations to a similar extent suggesting that the taxonomic composition remains little affected. Bacterial biomass (direct microscopy) showed the same pattern as microbial biomass (C_{mic}) and bacterial PLFAs. However, bacterial biomass as measured by image analysis represented only 12-15% of microbial biomass; similar ratios have been reported before (Jenkinson et al. 1976).

Soil fauna

Among microfauna, bacterivorous and plant feeding nematodes dominated in each of the systems; fungivorous nematodes were far less abundant. Despite their low abundance, fungivorous nematode densities were 43% higher in the two conventional systems than in the organic systems. This was unexpected since fungal marker PLFA indicates low fungal biomass in the CONMIN system and

fungivorous nematodes in grasslands are assumed to be more sensitive to intensive farming practices than bacterial feeders (Mulder et al. 2003). Presumably, the fungi dominating in the conventional systems were of high food quality, or the fungivorous nematodes used alternative food sources such as root hairs (Yeates and Bongers 1999). In contrast to fungivorous nematodes, the densities of omnivorous nematodes and enchytraeids were lowest in the CONMIN system. Assuming that omnivorous nematodes live on microorganisms and organic residues, this is consistent with low microbial biomass and lack of organic input to this system. Compared to the conventional systems herbivorous nematodes were on average 33% more abundant in both organic systems suggesting that they directly benefited from reduced pesticide application or from an increased root system resulting from root nutrient foraging in the organic systems (Andrzejewska 1976).

Herbicides and the molluscicide applications in 2003 and 2004 did not have detectable negative impact on earthworms and nematodes, as the density of earthworms and the three most abundant nematode feeding groups did not differ between the CONFYM system which received pesticides and the organic systems which did not. Similarly, Iglesias et al. (2003) reported that even high doses of molluscicides (metaldehyde pellets) did not negatively affect soil animal communities.

Nematode communities tended to be more diverse in systems receiving FYM. However, differences were not statistically significant and suggesting that decomposer diversity in general responds little to the input of more complex litter resources (Salamon et al. 2004, Wardle 2005). Earthworms benefited from organic fertilizer (cf. Pfiffner 1993, Marhan and Scheu 2005) and the increased abundance might have contributed to the enhanced microbial activity and biomass through incorporation of litter materials into the soil (Tiunov and Scheu 2000, Haynes et al. 2003). Density of Diptera larvae and enchytraeids was increased in both organic systems but was low in both conventional systems. This suggests that NPK fertilizer and/or pesticide application in the CONFYM system suppressed Diptera and enchytraeids. In fact, Salminen et al. (1996) showed that mortality rates of enchytraeids are high when exposed to a commercial herbicide preparation.

Aboveground fauna

Aphids were almost twice as abundant in systems which received mineral fertilizer and herbicides (CONMIN and CONFYM). It is known that aphid development heavily relies on plant nitrogen supply (Schütz et al. 2007) and increased nitrogen concentration in conventionally managed crops therefore likely results in higher aphid abundance (Nevo and Coll 2001, Gurr et al. 2004, Altieri and Nichols 2003). The predator community was dominated by spiders, and staphylinid and carabid beetles, but only spiders responded to farming systems.

Increased activity densities of agrobiont spiders in organically managed systems is often attributed to increased vegetation coverage (Feber et al. 1998, Schmidt et al. 2005), which is unlikely to be true in our study as vegetation coverage was on average 16% higher in the conventional systems. Web-building spiders attach their webs to the vegetation and therefore benefit from increased availability of suitable web sites (Rypstra et al. 1999). The higher density of web-building spiders in both organic systems therefore likely resulted from increased weed density (see also Pfiffner and Luka 2003). Similar to web-building spiders, the density of surface-active spiders was increased in organic systems, however, this likely resulted from increased prey availability. Diptera larvae were the only analyzed prey taxon that mirrored the response of spiders to fertilization suggesting that they contributed to spider diets (cf. Nentwig 1987, Nyffeler 1999). Some spider species prey frequently on aphids, as indicated by recent molecular studies (Harwood et al. 2004). In addition to increased nutrient availability, reduced spider abundance therefore likely contributed to the high density of aphids in systems receiving mineral fertilizers. Similarly, Östman et al. (2001) demonstrated that aphids were more successfully suppressed by natural enemies in organic as compared to conventional farming systems. Overall, the investigated farming systems affected the aboveground fauna including herbivore pest species, even though effects were less pronounced than in the belowground system. This less pronounced response may have resulted from small plot size since invertebrates above the ground are more mobile than those belowground. Effects of farming systems on aboveground invertebrates likely resulted from both, increased nutrient supply to plants in conventional systems and fostering of herbivore control by generalist predators in organic farming systems.

Conclusions

We demonstrated that farming systems in the long-term strongly affect soil chemical, microbial and faunal characteristics, as well as the aboveground animal community. Organic farming fostered internal nutrient cycling and therefore contributed to more sustainable management. Application of farmyard manure increased the resource basis for belowground communities and beneficially affected the activity and biomass of decomposer biota. In a number of soil chemistry and soil biota characteristics the combined application of mineral (NPK) and organic (FYM) fertilizer appeared to counteract the beneficial effects of organic fertilizer addition. The type of organic fertilizer (composted or rotted manure) affected soil pH, but effects on the other analyzed parameters were similar despite the amount of carbon added in rotted manure was 20% less than that in compost. The aboveground animal community also responded to farming systems but compared to belowground biota the response was less pronounced. The results suggest that NPK fertilizer application increase the density of a major pest (aphids) whereas increased generalist predator abundance in organic farming systems reduces pest density. Overall, the results suggest that organic farming significantly improves decomposer performance, internal nutrient cycling and biological control of pest species thereby contributing to more sustainable land use.

Chapter 3 - Generalist predators in long-term organically and conventionally managed grass-clover fields: implications for conservation biological control

3.1. ABSTRACT

Farming systems affect generalist predator communities, with negative effects of insecticide application and tillage in conventionally managed monocultures. Effects of fertilization regimes on generalist predators in frequently disturbed agroecosystems have received considerably less attention. We analyzed the seasonal dynamics of spiders (Araneae), ground beetles (Carabidae) and rove beetles (Staphylinidae) in conventionally and organically managed grass-clover fields that received farming-system specific treatments for at least 20 years. Conventional management significantly reduced spider activity-density early and late in the growing season. Ground-active spiders were affected most, with *Pardosa* (Lycosidae) individuals benefiting from organic management. We analyzed the role of this genus in suppressing herbivore numbers in a field experiment late in the season. Removal of *Pardosa* had no short-term effect on any prey taxa; however, spider guild structure changed significantly. Ground- (excluding *Pardosa*) and foliage-running spiders were significantly more abundant in plots without *Pardosa*. We suggest that the lack of differences in prey abundance between plots with high and reduced *Pardosa* abundance may be a consequence of compensatory changes. In the presence of fewer *Pardosa*, ground- and foliage-running spiders were more abundant; therefore, their combined impact on herbivore numbers may have been elevated, cancelling increases in herbivores due to reduced predation by *Pardosa*. Our results indicate positive effects of organic farming on generalist predators, yet the implications of such elevated numbers are not easy to predict, as our field experiment failed to find evidence that one of the more clearly affected spiders reduced herbivore numbers.

3.2. INTRODUCTION

Organic farming practices focus on minimizing environmental damage while ideally maintaining economic feasibility (Vandermeer, 1995). Because pesticide use is generally prohibited by organic farming guidelines, one important pest management practice is conservation biological control, the fostering of natural enemy populations (Barbosa, 1998; Zehnder et al., 2007). Generalist predators are important biological control agents in several agroecosystems (Symondson et al., 2002) and agricultural management practices affect their abundance and diversity (Thorbek and Bilde, 2004; Navntoft et al., 2006). Several studies indicate a positive impact of organic management on carabid and spider activity-density (Feber et al., 1998; Mäder et al., 2002; Shah et al., 2003; Pfiffner and Luka, 2003), with a few studies showing contrasting negative effects on ground beetles (Carabidae: Moreby et al., 1994; Weibull et al., 2003) and rove beetles (Staphylinidae: Krooss and Schaefer, 1998; Shah et al., 2003) in cereals. Beneficial effects are mainly attributed to reduced mortality and richer weed flora in response to restricted pesticide use. In contrast to effects on generalist predator activity-density, effects of the farming system on species diversity of generalist predators are less predictable. Both species and functional group diversity of carabids and spiders can either be enhanced (Gluck and Ingrisch, 1990; Basedow, 1998; Kromp, 1999; Fuller et al., 2005), reduced (Weibull et al., 2003) or remain unaffected (Purtauf et al., 2005; Schmidt et al., 2005) by organic farming. Besides landscape and management effects (Clough et al., 2005; Purtauf et al., 2005; Schmidt and Tscharntke 2005 Bianchi et al., 2006), local soil characteristics (Irmler, 2003) as well as different farming-system histories (Booij and Noorlander, 1992) contribute to such contradictory results. The study by Booij and Norlander (1992) further suggests that crop type is even more important in forming generalist predator communities than management strategy. Grass-clover agroecosystems are more diverse agroecosystems than crop monocultures and are characterized by a higher frequency of disturbance as a consequence of multiple cuttings during a single growing season. Little is known about the impact of management strategy on generalist predator population dynamics in such frequently disturbed and diverse agroecosystems (but see Thomas and Jepson, 1997; Haysom et al., 2004).

Assuming a beneficial effect of organic farming on density and diversity of some generalist predator taxa, it remains questionable if pest suppression is necessarily improved. Generalist predators

frequently prey on individuals from their own feeding guild (intraguild predation, Rosenheim, 1995), and such feeding behavior could limit their effectiveness in suppressing pests at increased abundance (Snyder and Wise, 1999; Prasad and Snyder, 2006). Species that benefit from organic farming could be functionally redundant in terms of pest suppression or could negatively affect other pest-consuming predators. Spiller (1986) suggested such a negative effect of greater predator diversity, based upon his finding that a single web-building spider suppressed prey more effectively than in combination with a second web-building spider species. In contrast, Provencher and Riechert (1994) and Riechert and Lawrence (1997) manipulated spider species richness in field-cage experiments and found that herbivore abundance was negatively correlated with increasing predator diversity. Lang (2003) removed ground beetles from cages in winter wheat resulting in a two-fold increase of wolf spider (Lycosidae) abundance. Aphid and Thysanoptera prey responded differently depending on the identity of the removed predator functional group (Carabidae or spiders) and time of sampling. Cardinale et al. (2003) showed a positive effect of multi-predator species assemblages on aphid suppression in alfalfa, a response not observed in any single-predator species treatment (coccinellid beetles, predatory bugs or parasitic wasps). Clover species have several economically important pests, including virus-transmitting aphids (Pons et al., 2005) and weevils (Coleoptera: Curculionidae) (Murray and Clements, 1995). To date it remains unclear which generalist predator groups contribute to herbivore suppression in such frequently disturbed agroecosystems (but see Milne and Bishop, 1987; Elliott et al., 2002).

We analyzed the surface-active generalist predator fauna (Araneae, Carabidae and Staphylinidae) of grass-clover meadows under organic and conventional farming within a replicated plot-scale agricultural long-term trial (DOK trial, Switzerland). We expected (i) intense seasonal fluctuations, (ii) a long-lasting impact of cutting on all analyzed taxa and further expected (iii) a positive impact of organic farming on generalist predator abundance and diversity. In a field experiment at the end of the growing season, we tested whether one of the predators favored by organic farming had an impact on pests in organically managed grass-clover systems. We expected reduced herbivore suppression if this species, which benefited from organic management, were excluded from fenced plots.

3.3. METHODS

Study site and sampling protocol

The DOK trial (bioDynamic, bioOrganic, Konventionell) in Therwil, Switzerland is an agricultural long-term experiment established in 1978 by the Agroscope Reckenholz-Tänikon research station (ART) and the Research Institute of Organic Agriculture (FiBL) to compare organic and conventional farming systems and their impact on soil and aboveground processes. The fourth crop rotation period started in 1999 with potatoes followed by wheat, soybeans, maize and ended with two years of grass-clover in 2004 and 2005. We sampled the temporary grass-clover plots 2004 in the organic (BIOORG) and the conventional system mimicking stockless farming (CONMIN, see table 3.1.).

Table 3.1. Farming systems sampled in the DOK-Trial in Therwil, Switzerland. Terms and abbreviations given in this table are used throughout the text. Fertilizer (farmyard manure = FYM, synthetic = NPK). Table modified from Fließbach et al. (2007).

	Bioorganic	Mineral
Abbreviation	BIOORG	CONMIN
Organic fertilizer	rotted FYM, aerated slurry	-
Inorganic fertilizer	-	NPK
Weed control	mechanical	mechanical & chemical
Disease control	indirect methods	chemical (threshold)
Pest control	plant extracts	chemical (threshold)

Crop rotation and soil tillage regime were identical in both farming systems and all 5x20 m large plots had been under the same farming system for 26 years. Synthetic insecticides were last applied to the CONMIN subplots in 1999 and soils of this system were last treated with a molluscicide in 2001 and 2002. The soil is a haplic luvisol on deep deposits of alluvial loess. Mean precipitation is 785 mm per year with an annual average temperature of 9.5°C (Fließbach et al., 2007). Grass-clover plots were cut every 47±3 days between 30 April and 3 November resulting in 5 cuttings per year.

Fenced enclosures (1.8 m², 50 cm-high plastic barriers inserted 10 cm into the soil, open on top) were established at randomly chosen locations at five consecutive dates between cuttings (see table 3.2.).

Table 3.2. Management practices and sampling intervals in grass-clover plots of organic (BIOORG) and conventional (CONMIN) farming systems in 2004. Note that no pesticides were applied to grass-clover plots in the sampling year.

Date	Measure	BIOORG	CONMIN	Unit
18 Mar	1st FYM application	20	-	m^3/ha
	NPK application	-	40	kg N/ha
		-	40	kg P/ha
		-	274	kg K/ha
06 Apr-20 Apr	1st sampling	+	+	
30 Apr	1st cutting	+	+	
7 May	2nd FYM application	20	-	m^3/ha
	2nd lime application	-	30	kg N/ha
16 May-30 May	2nd sampling	+	+	
10 Jun	2nd cutting	+	+	
14 Jun	3rd FYM application	20	-	m^3/ha
	3rd lime application	-	30	kg N/ha
30 Jun-14 Jul	3rd sampling	+	+	
26 Jul	3rd cutting	+	+	
28 Jul	4th lime application	-	30	kg N/ha
14 Aug-28 Aug	4th sampling	+	+	
9 Sep	4th cutting	+	+	
01 Oct-15 Oct	5th sampling	+	+	
3 Nov	5th cutting	+	+	

Four pitfall traps were placed along the inner barrier and one trap was located at the centre, with all traps containing a water-detergent mix (traps: 7 cm diameter, 11 cm height). After 14 days all pitfall samples were transferred to 70% ethanol and later hand sorted for carabids, rove beetles and spiders. Adult spiders and carabids were identified to species level (Araneae: Heimer and Nentwig, 1991; Carabidae: Müller-Motzfeld, 2004), staphylinids only to subfamily level (Freude et al., 1964).

Potential prey (Aphididae, Auchenorrhyncha and sminthurid and entomobryid Collembola) was sampled at the last sampling date in October. Aphid, Auchenorrhyncha and Sminthuridae densities were estimated by suction sampling a separate 2-m² area within each plot for 2 min (fenced with a plastic barrier, 50 cm high, EcoVac Insect suction sampler, EchoTech, Germany). Entomobryid Collembola were extracted from a soil core (20 cm diameter) using a modified heat extraction system (Kempson et al., 1963). Five randomly located measures of vegetation height and one estimate of plant cover were taken from every fenced enclosure at the end of all sampling periods.

Field experiment

The field experiment was carried out from 29 September to 28 October 2004 in four replicated, organically managed grass-clover subplots with moderate fertilizer intensity. Two fenced enclosures (1.8 m², 50 cm high plastic barriers inserted 10 cm into the soil, open on top) were established in each plot with a minimum distance of 3 m to the plot edge and between enclosures. *Pardosa* wolf spiders (Lycosidae) were removed daily from all enclosures by hand searching (10 min per plot, twice a day) and 5 pitfall traps (without preservative) for 7 days. On average 25±3 (SE) *Pardosa* individuals were removed from each enclosure. All individuals were kept in plastic cups with a plaster-of-Paris base with water and one *Drosophila melanogaster* (curly; b.t.b.e Insektenzucht GmbH, Germany) given every second day.

At the end of the removal period, one enclosure per plot received 25 randomly chosen *Pardosa* individuals (treatment SD - standardized natural density); no *Pardosa* were reintroduced into the second enclosure (treatment RD - reduced density). All enclosures were left undisturbed for 17 days, at which time they were sampled again with 5 pitfall traps for 7 days, and shortly before the next cutting date, with a suction-sampler for 3 minutes. Samples were sorted to species level for adult spiders (taxonomy followed Platnick, 2006) and to family or subfamily level for selected arthropods. The time available for this field experiment was restricted by the intervals between cuttings.

Data Analysis

Repeated-measures (RM) ANOVA with farming system as fixed factor was performed for dependent variables including the activity-density of all analyzed generalist predator taxa, spider guild structure and vegetation characteristics at the five consecutive sampling dates. The decision for univariate analysis instead of RM MANOVA was based on Scheiner and Gurevitch's (2001, p.155) citation of Maxwell and Delany (1990), stating the limited Power of RM MANOVA at small sampling size. Within-subjects probabilities were corrected by Huynh-Feldt adjustments as recommended by Potvin et al. (1990) and Ott (1993). In case of a significant interaction between sampling date and farming system, one-way ANOVA were performed to analyze farming system effects on single dates. In case of a significant factor sampling date, Bonferroni corrected post-hoc tests were performed to identify

differences between dates. Dominant spider and carabid species, and staphylinid subfamilies (min. 30 individuals for all categories), were ordinated with log-transformed abundance data. Principal components analysis (PCA) calculated the sample scores of each taxon and related those coordinates to farming system (coded as environmental variable and displayed as centroids in Fig. 3.3.; ter Braak and Smilauer, 2002). Farming-system effects on prey taxa were analyzed by MANOVA with log-transformed abundance data as dependent, and farming system as independent, variables. Relationships between predator and prey activity density and vegetation characteristics were analyzed by nonparametric Spearman rank-order correlation.

Spider guild structure in the field experiment was analyzed by MANOVA using the experimental treatment (*Pardosa* removal) as the independent variable and abundances of four guilds (ambushers, foliage runners, ground runners, sheet-web weavers) as the dependent variables. Guilds were defined after Uetz et al. (1999) with the exceptions of *Oedothorax* sp. (Linyphiidae) and *Phrurolithus festivus* (Corinnidae), which were classified as ground runners after Alderweireldt (1994b), Thornhill (1983) and Boeve (1992); and *Pachygnatha* sp. (Tetragnathidae), which was classified as a foliage runner after Harwood et al. (2005). In case of a significant MANOVA, ANOVA was performed for each single guild. All activity-density data were $\log_{10}(x+1)$ transformed to improve homogeneity of variance and Pillai's criterion was used to test for significance of main effects and interactions in multivariate analysis (Scheiner and Gurevitch, 2001). All means are expressed ± standard error. Statistical analyses were calculated using Statistica 7.1. (StatSoft, Germany).

3.4. RESULTS

Effects of farming system

Over five consecutive samplings during the approximately 6-month sampling period, 1424 spiders (36 species), 209 ground beetles (23 species) and 288 rove beetles (6 subfamilies) were trapped. Only sampling date had a significant effect on the abundance of carabids (Fig.3.1.a; RM ANOVA; H-Fε=0.98, $F_{4,24}$=4.80, P=0.006) and staphylinids (Fig.3.1.b, RM ANOVA; H-Fε=1.00, $F_{4,24}$=8.76, P<0.001).

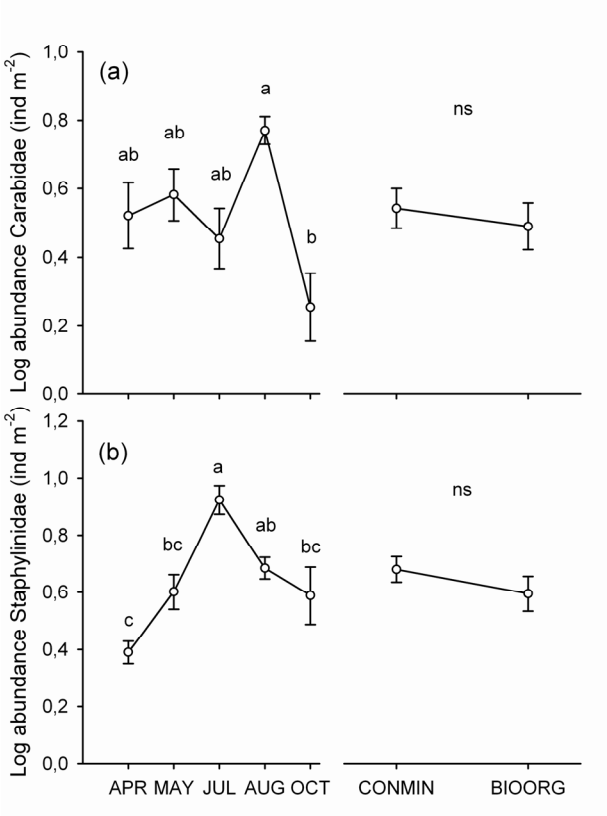

Figure 3.1. Log activity-density of (a) Carabidae and (b) Staphylinidae as affected by sampling date (April – October) and farming system (CONMIN = stockless conventional farming, BIOORG = organic farming). Small letters indicate significant differences (Bonferroni post-hoc), error bars give ± one standard error.

In contrast, spider activity-density varied with both sampling date and farming systems (Fig.3.2.; RM ANOVA; farming system x date: H-Fε=0.72, $F_{3,17}$=3.64, P=0.035). Spider activity-density was on average 80 % higher in organically managed fields in April (one-way ANOVA; $F_{1,6}$=13.30, P<0.011) and in October (one-way ANOVA; $F_{1,6}$=7.65, P<0.033), with no significant treatment effect on all other sampling dates.

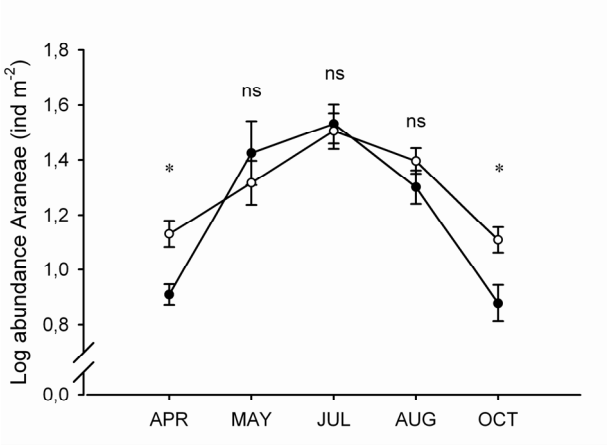

Figure 3.2. Log activity-density of adult and immature spiders in organically (BIOORG:○) and conventionally managed plots (CONMIN:●) for all five sampling dates. Asterisks indicate significant differences at each date (ANOVA), error bars give ± one standard error.

Pooled spider diversity tended to be higher in organically managed grass-clover plots, with a Shannon-Wiener index of 1.5±0.1 in conventional plots and 1.7±0.1 in organically managed plots (one-way ANOVA; $F_{1,6}$=5.52, P=0.057). In conventional plots 95% of the adult spiders belonged to the 15 most-abundant species, while in organically managed plots 95 % of the adults belonged to the 18 most-abundant species. Guild structure within the spider community differed between conventionally and organically managed systems. Sheet-web weaver activity-density differed between sampling dates (RM ANOVA; H-Fε=1.00, $F_{4,24}$=47.35, P<0.001) with peaks between May and August. Ambusher activity-density indicated a similar trend (RM ANOVA; H-Fε=1.00, $F_{4,24}$=2.67, P=0.056) with lowest activity densities in April. Ground-running (RM ANOVA; farming system x date: H-Fε=1.00, $F_{4,24}$=2.95, P=0.041) and foliage running spider activity-density (RM ANOVA; farming system x date: H-Fε=0.95, $F_{4,23}$=3.57, P=0.022) differed significantly between farming systems and sampling dates. Foliage running spiders had significantly higher activity-densities in conventionally managed fields in May (one-way ANOVA; $F_{1,6}$=56.29, P<0.001). Ground runner activity-density was significantly higher in organically managed plots in April (one-way ANOVA; $F_{1,6}$=6.55, P=0.043), August (one-way ANOVA; $F_{1,6}$=7.73, P=0.032) and October (one-way ANOVA; $F_{1,6}$=6.25, P=0.046).

PCA indicates a preference of the most common non-web-building spiders for organically managed plots, while species of the common staphylinid subfamilies were characteristic for conventionally managed plots (Fig. 3.3.).

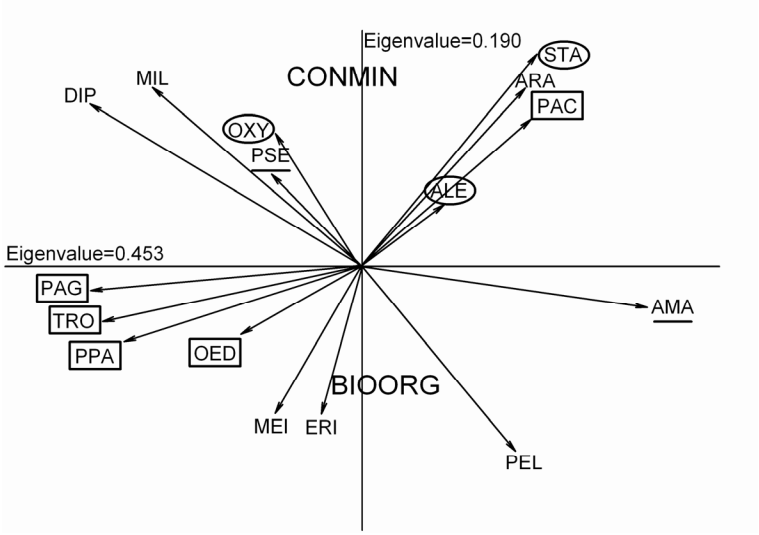

Figure 3.3. Principle component analysis of dominant predator taxa (min 30 individuals), showing species-sample scores in relation to farming system (coded as environmental variable and displayed as centroids). Rectangles = non-web-building spider species, Ellipse = staphylinid subfamilies, underlined = carabid species, no mark = web-building spider species. ALE, Aleocharinae; AMA, *Amara* sp.; ARA, *Araeoncus humilis*; DIP, *Diplostyla concolor*; ERI, *Erigone dentipalpis*; MEI, *Meioneta rurestris*; MIL, *Milleriana innerans*; OED, *Oedothorax apicatus*; OXY, Oxytelinae; PAC, *Pachygnatha degeeri*; PAG, *Pardosa agrestis*; PPA, *Pardosa palustris*; PEL, *Pelecopsis parallela*; PSE, *Pseudophonus rufipes*; STA, Staphylininae; TRO, *Trochosa ruricola*.

Individuals of *Pardosa* sp. formed 78% of all ground-running spiders, and the pooled activity-density of immatures of this genus was on average 3.3 times higher in organically managed grass-clover plots (one-way ANOVA; $F_{1,6}$=6.45, P=0.044). Six non-web-building spider species were only found in organically managed plots [*Alopecosa pulverulenta* (Clerck), *Aulonia albimana* (Walckenaer), *Evarcha* sp. imm., *Ozyptila simplex* (Cambridge), *Pardosa amentata* (Clerck), *Pisaura mirabilis* (Clerck)], with one cursorial and two web-building species sampled only in conventional plots [*Tibellus oblongus* (Walckenaer), *Tiso vagans* (Blackwall), *Porrhomma* sp.]. Carabid species presence/absence data is not shown, as capture numbers over the sampling period were generally low.

None of the analyzed herbivore (1565 individuals) or decomposer (324 individuals) prey taxa was influenced by farming system in October (MANOVA; $F_{4,3}$=1.31, P=0.430). Also, farming system did not significantly affect aphids (14±6 ind. m^{-2} in CONMIN and 71±38 ind. m^{-2} in BIOORG),

Auchenorrhyncha (117±20 ind. m^{-2} in CONMIN and 125±13 ind. m^{-2} in BIOORG), sminthurid Collembola (45±22 ind. m^{-2} in CONMIN and 19±12 ind. m^{-2} in BIOORG) and entomobryid Collembola (1512±578 ind. m^{-2} in CONMIN and 756±368 ind. m^{-2} in BIOORG).

Comparing densities of predators and potential prey for all plots pooled, reveals two statistically significant relationships. Collembola abundance was negatively correlated with ground beetle densities (N=8, r_s=-0.889, P=0.003); in contrast, there was a positive correlation between spider and Collembola abundance (N=8, r_s=-0.801, P=0.017). No significant correlations were found between aphid densities and any predator group.

Vegetation height (27.5±2.1 and 25.8±2.2 cm in organically and conventionally managed plots, respectively) was only affected by sampling date (RM ANOVA; H-Fε=1.00, $F_{4,24}$=96.62, P<0.001). Estimated plant coverage differed significantly between organic (88±2%) and conventional (85±3%) grass-clover plots depending on sampling date (RM ANOVA; farming system x date: H-Fε=1.00, $F_{4,24}$=5.44, P=0.003), with a significantly higher coverage in organically managed plots in October (Fig. 3.4.; one-way ANOVA; $F_{1,6}$=11.54, P=0.015).

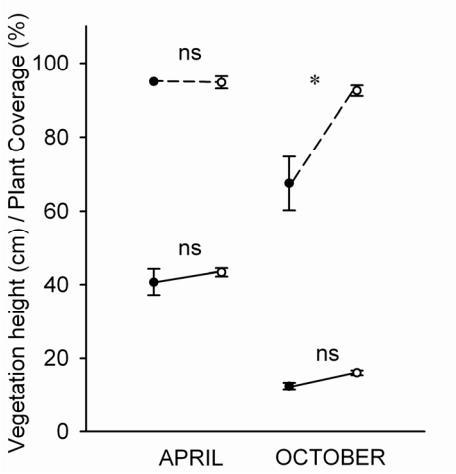

Figure 3.4. Plant coverage (dashed line) and vegetation height (solid line) in conventionally (CONMIN: ●) and organically (BIOORG: ○) managed grass-clover plots at sampling dates with significant treatment effects on spider abundance (April & October). Asterisks indicate significant differences at each date (ANOVA), error bars give ± one standard error.

Spider activity-density and plant coverage were correlated only at this sampling date (N=8, r_s=0.788, P=0.020). Carabid activity-density was generally correlated with vegetation height (N=40, r_s=-0.341, P=0.032), and staphylinid activity-density was negatively correlated with both vegetation

coverage (N=40, r_s=-0.470, P=0.002) and vegetation height (N=40, r_s=-0.489, P=0.001) over the entire sampling period.

Field experiment

The *Pardosa* density-treatment was maintained for the entire experiment; after 17 days, about one-third as many wolf spiders were trapped in RD as SD enclosures (1.8±0.5 and 5.0±2.0, respectively; $F_{1,3}$= 15.92, P=0.028). In total 2268 insects and 956 spiders from 24 species (only adults) were analyzed, but the activity-densities of abundant taxa of insect predators (Carabidae: 6±2 ind m^{-2} in RD plots and 8±4 ind. m^{-2} in SD plots; Staphylinidae: 34±5 ind. m^{-2} in RD plots and 38±4 ind. m^{-2} in SD plots), herbivores (Auchenorrhyncha: 115±20 ind. m^{-2} in RD plots and 118±12 ind. m^{-2} in SD plots; Aphididae: 32±13 ind. m^{-2} in RD plots and 24±9 ind. m^{-2} in SD plots) and decomposers (entomobryid Collembola: 1568±324 ind. m^{-2} in RD plots and 1407±296 ind. m^{-2} in SD plots) were not affected by *Pardosa* removal (MANOVA; $F_{5,2}$=0.13, P=0.726).

In contrast, removing *Pardosa* did affect spider guild structure (MANOVA; $F_{4,3}$=11.59, P=0.036). Ground-running spiders (excluding the manipulated *Pardosa* sp.) were 6.5 times more abundant in RD than SD enclosures (Fig. 3.5.; one-way ANOVA; $F_{1,6}$=15.48, P=0.008).

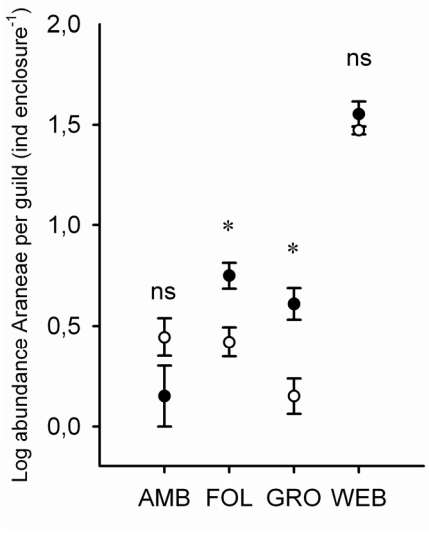

Figure 3.5. Log activity-density of adult spiders per guild (AMB: ambushers, FOL: foliage runners, GRO: ground runners without *Pardosa* sp. and WEB: sheet-web weavers) in enclosures with reduced (RD: ●) and with standardized (SD: ○) *Pardosa* densities. Asterisks indicate significant differences between farming systems (ANOVA), error bars give ± one standard error.

The density of two foliage-dwelling species (*Pachygnatha clercki* Sundevall and *Pachygnatha degeeri* Sundevall) was on average 2.7 times higher in RD than SD enclosures (one-way ANOVA; $F_{1,6}$=11.20, P=0.015). Ambusher and sheet-web weaver abundance was not affected by removing *Pardosa*.

3.5. DISCUSSION

Ground-running spiders were more sensitive to farming system than other spider guilds (foliage runners, ambushers, sheet-web weavers) or predatory beetles (Carabidae and Staphylinidae). Because no insecticides were applied to our studied grass-clover plots in 2004, mortality caused directly by pesticides is unlikely. Farming-system effects, most prominent for lycosids and gnaphosids, were most pronounced early (April) and late (October) in the growing season, and were correlated with differences in vegetation characteristics in our grass-clover meadow. This interpretation results from a significant farming-system effect on vegetation parameters and a positive correlation between vegetation coverage and spider activity-density in October. Other farming system comparisons also suggested increased spider abundance in response to higher plant coverage under organic farming (Feber et al., 1998; Pfiffner and Luka, 2003; Schmidt et al., 2005). Nevertheless, we did not find any significant correlation between vegetation characteristics and spider abundance or any treatment effect on vegetation in April. As we documented a significant farming-system effect on spider activity-density for this date, other factors must have contributed to the positive response of spiders to organic farming early in the growing season.

If analyzed independently of farming system, spiders and decomposer prey are positively correlated, indicating a numerical response to increased prey availability. Recent molecular studies provide evidence for strong feeding links between spiders and the decomposer subsystem (Agusti et al., 2003). In contrast, predator numbers were not correlated with aboveground herbivore prey. Contrasting opinions exist about the role of aphid prey for generalist predators. Although molecular studies show consumption of aphids by spiders (Harwood et al., 2005) and carabids (Harper et al., 2005) and field experiments documented aphid predation by generalist predators (e.g. Losey and Denno, 1998; Schmidt et al., 2004), several aphid species are low-quality or even toxic prey for some

generalist predator species (for review see Toft, 2005). Indications of a positive numerical response of spiders to experimentally enhanced levels of decomposer prey come from studies in forests (Chen and Wise, 1999, Miyashita et al., 2003), vegetable gardens (Halaj and Wise, 2002; Wise et al., 2006) and winter wheat (Birkhofer et al., submitted). We therefore suggest that a positive response of spiders to organic farming in grass-clover meadows is not only a consequence of increased structural complexity and plant diversity, but also due to higher prey availability from the decomposer subsystem.

A positive impact on Collembola caused by the addition of organic matter and reduced tillage is documented for agroecosystems (Moreby et al., 1994). Such effects on decomposer abundance are not indicated by our estimation of prey availability in October. Nevertheless, spiders were approximately twice as abundant in organic plots in October, and enhanced predation rates on Collembola might mask differences of decomposer prey in the analyzed farming systems. If spiders in our organic plots benefited from increased decomposer prey availability in April, pest-control potential could be optimized through this alternative prey. Many pests, e.g. aphids, colonize arable fields early in the growing season (Lang et al., 2003); thus, already established and abundant generalist predator communities could be more efficient in limiting pest population growth (Scheu, 2001).

Principal components analysis indicates species/subfamily-specific responses to the analyzed farming systems. The higher Shannon-Wiener index for spiders in organically managed plots supports the results of the PCA, indicating that more species were characteristic for organic plots. Synthetic fertilizer, as applied in the conventional system, detrimentally affects several arthropod taxa (e.g. Yardim and Edwards, 2003). The higher diversity in organically managed plots could be either a result of direct negative effects on spider species, or it could indicate a negative impact on potential prey resulting in a less diverse spider community. In contrast to spiders, all three common staphylinid beetle subfamilies (Aleocharinae, Staphylininae and Oxytelinae) had higher activity-densities in conventional managed plots, a result that is in line with earlier studies on this generalist predator group (Krooss and Schaefer, 1998; Weibull, 2003). Rove beetle abundance correlated negatively with vegetation height and cover, whereas carabids were captured more frequently in plots with higher vegetation. The unspecific response of *Amara* sp. to different farming systems potentially reflects its granivorous feeding behavior (Holland, 2002), and the temporally restricted differences between

vegetation characteristics in conventional and organically managed fields. Pfiffner and Niggli (1996) found an approximately 10 times higher abundance of *Amara* individuals in organic farming systems compared to conventionally managed winter wheat plots at the DOK trial. In contrast to their wheat fields, our grass-clover plots received no herbicides in 2004. Weed abundance and diversity might therefore not show comparable strong contrasts between organic and conventional plots and therefore should not favor granivorous species in a specific farming system.

Consecutive cuttings did not result in a steady decline of generalist predator numbers; in contrast, predator activity-density peaked after two (spiders and rove beetles), or three (carabids) cuttings. As these generalist predators are highly mobile, recolonization rates are certainly favored by small plot sizes in the DOK trial and partially counteract negative effects of cutting demonstrated at the field scale (spiders: Thomas and Jepson, 1997; Thorbek and Bilde, 2004; Carabidae: Haysom et al., 2004; Staphylinidae: Good and Giller, 1991). Nevertheless, most large-scale studies also documented a quick recovery of generalist predator populations from cutting (Howell and Pienkowski, 1971; Good and Giller, 1991; Thomas and Jepson, 1997).

Pardosa benefited most from organic management in our study. We therefore conducted a field experiment to analyze the impact of this taxon on prey and predator communities in organic fields. We did not find a short-term effect of *Pardosa* removal on any analyzed insect group (predators, herbivores and decomposer). Wise (2004) documented increased population growth of Collembola in response to experimentally reduced spider abundance in a forest system. Studies in agroecosystems traditionally focused on herbivore prey and less diverse agroecosystems (crop monocultures). Schmidt et al. (2003) studied the impact of generalist predator and specialist predator removal on aphid populations and uncovered higher aphid control potential through specialists (parasitoid wasps). Lang et al. (1999) and Lang (2003) demonstrated a significant positive effect of lycosid removal on certain herbivore groups in maize and winter wheat. Spider removal also resulted in significantly higher herbivore abundance when compared to single spider species treatments or spider assemblages in an old-field (Riechert and Lawrence, 1997). The low impact of predator removal in our experiment could be a consequence of the limited experimental period (31 days from establishing treatments to the end of sampling) and/or high immigration rates of herbivores into plots independent of *Pardosa* treatment.

Another explanation for the limited effect of *Pardosa* removal on prey populations could be compensatory changes in the intensity of predation on prey. Effects of reduced predation by *Pardosa* on herbivore numbers could have been masked through increased predation rates by other generalist predators that increased in response to the *Pardosa* manipulation. Snyder and Wise (1999) earlier found evidence that lycosids depress densities of non-lycosid spiders in the ground layer of cucurbit crops. In our study, spider guild structure showed a strong response to *Pardosa* manipulation. Out of four analyzed guilds, foliage runners (mainly *Pachygnatha degeeri*) and ground-running species (excluding *Pardosa*, mainly Gnaphosidae and *Phrurolithus festivus*), were significantly more abundant in lycosid-removal enclosures. Both guilds share the same stratum with wolf spiders, with *P. festivus* being a surface-hunting, myrmecophilous species, and *P. degeeri* being a tetragnathid species that abandons web-building behavior as adult (Harwood et al., 2005). According to Boeve (1992) it is unresolved to what extent *P. festivus* really feeds on ants and no additional information on feeding preferences is available. *Pachygnatha degeeri*, a foliage- dwelling tetragnathid, preys heavily on aphids even at low prey densities (Harwood et al., 2005). We suggest that the absence of a lycosid-removal effect on potential prey was partially caused by increased abundance or activity of other surface-active spider species in response to fewer *Pardosa*. We further suggest that because of the short duration of this experiment, shifting intensities of intraguild predation more likely caused the pronounced differences than exploitative competition.

Conclusions

We demonstrated that organic farming can enhance the density and diversity of surface-active spiders in frequently disturbed grass-clover agroecosystems. This positive response of a major generalist predator group in part correlated with plant cover but early in the growing season it likely resulted from increased availability of decomposer prey. Such a predator-prey relationship may strengthen generalist predator communities for successful conservation biological control in times of pest colonization. High lycosid density, however, does not necessarily cause improved pest suppression in organic farming. Besides the possibility of generally low predation pressure on herbivores, absence of a strong effect on herbivore numbers could have resulted from intraguild

predation between spider functional groups. Other surface-active spider species were more abundant under experimentally reduced *Pardosa* numbers presumably neglecting any release from predation for herbivores. Effects of lycosid removal on cursorial and web-building spiders differed in this study, with species sharing a stratum with wolf spiders suffering from increased wolf spider abundance, which supports our IGP-based interpretation. Our results show the complexity of management, predator-prey and intraguild interactions in frequently disturbed agroecosystems. It is necessary to evaluate the extent of such interactions in organically managed agroecosystems as they affect conservation biological control and therefore the sustainability of agricultural management systems (Spiller, 1986; Rosenheim, 1998; Snyder and Wise 1999, 2001).

Chapter 4 – Small scale spatial pattern of web-building spiders in alfalfa: Relationship to prey availability, disturbance from cutting and intraguild interactions

4.1. ABSTRACT

Knowledge of factors influencing the large and small scale spatial distribution of web-building spiders in agroecosystems is directly relevant to predicting the effectiveness of this generalist predator group as biological control agents. In an alfalfa field, small scale spatial patterns of spider webs were analyzed over multiple scales to study the impact of prey distribution, disturbance from cutting and spider abundance on pattern formation. Before alfalfa was cut, aphid prey was aggregated. Spiders, however, did not show an aggregated distribution; in contrast, web owners had significantly fewer neighbors at short distances than expected under spatial randomness. Although cutting did not immediately change spatial relationships between web-builders, three weeks after cutting small-scale regularity had changed to a random web distribution at all analyzed scales. Regular spatial patterns were observed in times of maximum spider densities (before cutting) and highest spider recolonization rates (shortly after cutting). As we based our null-model distribution on the assumption of environmental heterogeneity, we propose that such small-scale regularity developed through intraguild interactions in times of increased activity of web-building and surface-active spiders. We conclude that the contribution of web-building spiders to biological control is not necessarily reduced through small-scale regularity. Spatial regularity occurred only during spider-density peaks and shortly after cutting, time periods that do not coincide with maximum rates of colonization by major agricultural pests.

4.2. INTRODUCTION

Spiders act as biological control agents in different agroecosystems (for reviews see Riechert and Lockley 1984, Wise 1993, Symondson et al. 2002, Nyffeler and Sunderland 2003), with web-building species preying on such economically important pest taxa as Aphididae and Auchenorrhyncha (Nyffeler et al. 1994). Alfalfa agroecosystems have several pests, with the potato leaf hopper, *Empoasca fabae* (Harris) (Auchenorrhyncha), and virus-transmitting aphid species being among the most destructive (Pons et al. 2005). Web-building spiders are abundant in alfalfa fields (Wheeler 1973) and may play an important role in limiting the population growth of aphids in agroecosystems (Marc et al. 1999). Utilizing spiders in conservation biological control depends upon knowing the relationship between prey consumption and spider density and distribution; thus, effective incorporation of web-building spiders in pest management strategies also requires knowledge of factors that limit spider density and determine the distribution of spiders within crop fields.

Spider populations in agroecosystems are generally disturbed by agricultural management practices, with known detrimental effects through tillage (Thorbek and Bilde 2004)), sowing (Öberg and Ekbom 2006) and insecticide application (e.g. Pekar 1999). Effects of cutting are compared to catastrophic events by Thomas and Jepson (1997), who document a 56-89% reduction in the population size of linyphiid spiders in recently cut grass lays. Despite this immediate negative effect, spider populations recovered quickly through aerial recolonization (ballooning). In contrast, Gudleifsson and Bjarnadottir (2004) did not measure any impact of cutting in hay fields, but instead attributed fluctuations of spider population size to temperature changes over the season. Howell and Pienkowski (1971) report a rapid decline of linyphiid abundance after cut alfalfa was removed from the field, but the population recovered to pre-harvest densities within a week.

In addition to investigating the numerical response to management practices and increased pest abundance (e.g. Elliott et al. 2002), ecologists have recently given considerable attention to the large scale spatial association between prey species and generalist predators. Carabid beetles and ground running spiders are among the most intensely studied groups, but results are contradictory, revealing species-specific and temporally unstable associations or even the absence of a spatial relationship with prey (Bryan and Wratten 1984, Warner et al. 2000, Winder et al. 2005, Pearce and Zalucki 2006).

Harwood *et al.* (2001a, 2003) found that web-building spiders (Linyphiidae) in winter wheat preferentially located their webs in patches with greater prey availability. Because many pest species (e.g. aphids) colonize crops early in the growing season, any delay between pest arrival and an increase in predator numbers would reduce their potential to suppress pest populations. A rapidly forming spatial association between aphid prey and predators could be more important than a numerical response *per se*. Such a change in spatial association might be of major importance for aphid control, as aphids are most successfully suppressed under certain threshold densities and when distribution is still limited to a few patches within crops (Marc et al. 1999, Lang 2003).

Intraguild interactions (competition and predation) are known to affect the abundance, distribution and community structure of generalist predators (Rosenheim et al. 1995). Samu *et al.* (1996) experimentally increased the availability of web sites for a linyphiid spider in wheat. Adult females apparently competed over these artificial web sites, with heavier individuals winning contests more frequently. Harwood and Obrycki (2005) showed in a laboratory study that competition for space influenced web size and web-site tenacity for three linyphiid species. Mortality did not differ in intra- and interspecific competition treatments, indicating comparable rates of cannibalism and intraguild predation. Further studies in non-agricultural systems have uncovered intra- and interspecific competition for web-site space (Spiller 1984, Toft 1987, Wise 1993, Heberstein 1998).

Few studies of solitary web-building spiders have focused on the analysis of spatial patterns over a range of distances [studies on burrow-living spiders are discussed elsewhere (Marshall 1997, Birkhofer et al. 2006)]. Small-scale aggregation in web-building spiders is often limited to juvenile life stages, with individuals later dispersing from the maternal web (for a review see Burgess and Uetz 1982). Riechert (1976) showed that web locations of the funnel web spider *Agelenopsis aperta* (Gertsch, 1934) reflect the distribution of suitable microhabitat sites at large scales, resulting in aggregations. Block-size analysis of density variance indicated regularity developing through territorial behavior at smaller block sizes. Hodge and Storfer-Isser (1997) documented aggregation as a result of conspecific cuing; individuals searching for web sites favored patches with webs over web-free areas, leading to clusters of spiders.

The current study describes small scale spatial patterns of spider webs in alfalfa over a range of scales and analyzes the relationship of pattern formation to management and biotic factors. In particular the study addresses the questions of whether or not (i) web distribution is associated to prey availability and if (ii) cutting and (ii) intraguild interactions affect the small scale distribution of spider webs in alfalfa.

4.3. MATERIALS AND METHODS

Study Site and Sampling

During five two-day survey periods between 14 September and 7 November 2005, 1224 spider webs (occupied and intact vacant webs) were located within 2 x 2-m plots (14 September and 4 October, N=5; other dates, N=4) inside an alfalfa field (University of Kentucky Spindletop Research Farm, Fayette County, Kentucky). A two-day survey period was defined to guarantee that spatial patterns at a given sampling date were formed by identical processes. Intact vacant webs were included in the analysis as abandoned sheet webs degenerate quickly (Toft et al, 1995, Schmidt et al. 2005). Plot size was chosen based on the pattern (spider web locations) under consideration. Plot size reflects the focus on small scale processes such as neighbor conflicts and small scale aggregation of spiders in response to locations with higher prey availability. Choice of size was further determined by methodological constraints, as recording webs without disturbance for yet not sampled webs within plots was impossible in larger areas.

New survey plots were randomly chosen on each survey date from a 3 x 8-plot grid, which was at least 20 m from the field edge and 6 m from other 3 x 8-plot grids. Each search for webs within a 4-m² plot lasted 3 - 4 h and was carried out using a water vaporizer to facilitate web detection. Spiders (N=684) were captured from occupied webs with an aspirator and adults (N=252) were determined to species using keys of Kaston (1948) and Ubick et al. (2005). Web-site characteristics (size, stratum and spider family) were recorded and locations were marked with a labeled flag. Five randomly located measurements of vegetation height were taken from all grids before Cartesian coordinates of all web locations were recorded. A wooden 2 x 2-m frame enclosed the survey area, with measurement tape fixed to two parallel sides indicating the Y coordinate. A right angled, 1-m ruler was used to record the

X coordinate after the area had been divided into two 2 x 1-m segments. The meadow was cut on 1 October and alfalfa was removed on 3 October. The first web survey was conducted 16 days before cutting, followed by a survey the day after alfalfa removal. Two further surveys were conducted weekly thereafter and a last survey was conducted 35 days after cutting.

The dominant web-building species in North American alfalfa fields belong to four families: Linyphiidae, Theridiidae, Tetragnathidae and Araneidae (Culin and Yeargan 1983a, b). Most species from these families build webs either on the soil surface or attached to low vegetation. The vegetation layer was dominated by two long-jawed orb weavers (Tetragnathidae), *Tetragnatha laboriosa* Hentz, 1850 and *Glenognatha foxi* (McCook, 1894), accounting for 8 and 10%, respectively, of all adults; the orb weaver (Araneidae) *Gea heptagon* (Hentz, 1850) (9% of all adults); and the sheetweb spider (Linyphiidae) *Florinda coccinea* (Hentz, 1850) (13%). The ground layer was dominated by the linyphiid species *Meioneta unimaculata* (Banks, 1892), *Tennesseellum formica* (Emerton, 1882) and *Erigone autumnalis* Emerton, 1882, accounting for 13, 36 and 5%, respectively. The above percentages are based on the total number of adult spiders collected in both strata.

Activity-density of wolf spiders (Lycosidae) was estimated using pitfall traps (white plastic cups filled with water, Ø=9.0 cm) in a neighboring part of the same alfalfa field. Six pitfalls were placed in three rows at 10, 20 and 30 m from the field edge with 6 m between traps. Traps were opened for two days during each web-survey period.

Spatial Analysis

Spatial patterns of point locations (in our case, web locations) can be assigned to one of three categories: aggregated, random or regular. As the category of spatial pattern exhibited can be a function of spatial scale (Wiens 1989), we chose a spatial-analysis technique, the O-ring statistic (Wiegand and Moloney 2004), to analyzes small scale patterns of web-building spiders over multiple scales. This technique requires knowing the coordinates of all points comprising the observed pattern. The distribution of available prey was analyzed with a count-based spatial statistic (SADIE, Perry 1998), because coordinate-mapping is impractical for non-stationary animals (Aphididae and Diptera). Choice of spatial analysis methods was based on the guidelines of Fortin et al. (2002) and Perry et al.

(2002). The following section briefly describes the techniques and provides the rationale behind specific analyses applied to our data.

The intensity of a pattern is the number of points (N) relative to the area mapped (A). Spatial-analysis software can redistribute the points of known intensity and pattern according to different null-model distributions. Any point, either observed or part of the pattern generated by a particular null model, can then be analyzed for the spatial relationship to all other points within this pattern. The O-ring statistic uses each point within a pattern as a focal location and calculates the number of points in rings of defined width around those focal points (ring width in this study = 10 cm). Ring distances to focal points increase stepwise, providing the O-ring statistic over scales with increasing distance. Results of O-ring analysis for an observed pattern do not by themselves provide information about the category of the pattern at different distances. To make inferences about the category of the observed pattern, a simulated reference distribution based on a null-model with identical intensity can be used to create confidence bounds for the observed pattern.

For our null model in spider-web analysis we chose a heterogeneous Poisson process, which models heterogeneity of plant distribution (Wildova 2004, Wijesinghe et al. 2005) based on the documented correlation of vegetational complexity and spider-web location (Janetos 1986, Riechert and Gillespie 1986, Uetz 1991, Dennis et al. 1998, Samu et al. 1999, McNett and Rypstra 2000). An example of areas with different probabilities of web occurrence based on a mapped pattern of spider webs is given in Fig. 4.1.

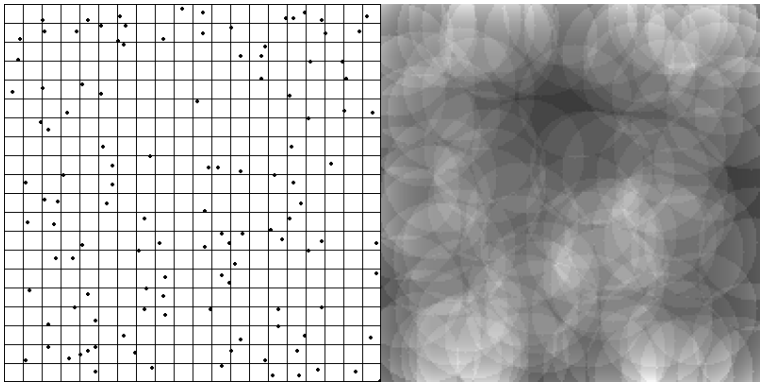

Figure 4.1. Example of a point pattern of spider webs inside a 4-m² grid on 14 September, showing the null-model distribution (heterogeneous Poisson process) based on the observed pattern. Dark areas represent areas with a lower probability of web occurrence than brighter areas.

To estimate web-site probability areas, a window of 30 cm radius is located around each observed location; the magnitude of overlap between such circles defines web-site probability. The relatively large window size is a conservative proxy for vegetation-caused habitat heterogeneity. Based on this probability distribution, the heterogeneous Poisson null model redistributes points 100 times and calculates the O-ring statistic for all replicates in order to estimate the 95% confidence envelopes (5^{th} highest and 5^{th} lowest simulation value, Stoyan and Stoyan 1994). When comparing O-ring statistics of observed and reference patterns, deviation from randomness at a given distance is indicated by the O-ring function crossing the confidence envelope -- regularity when crossing the lower boundary, aggregation when crossing the upper limit.

Besides a univariate analysis, in which all webs are assigned to the same pattern independent of web-site or web-owner characteristics, a bivariate analysis differentiates between two types of points. We analyzed the spatial relationship between webs of larger species (>5 mm) and webs of smaller species (<3 mm). While the univariate null model tests for spatial randomness between points, the bivariate null model tests for independent occurrence of the two different point patterns. Crossing envelopes in the bivariate analysis indicates repulsion between webs in the case of crossing the lower limit, attraction when crossing the upper envelope. Only data from 14 September (before cutting) had sufficient numbers of webs of larger species for a bivariate analysis. In order to correct for edge effects, data were analyzed for distances only up to a third of the shortest extent of the study area (Fortin and Dale 2005), with distances smaller than 4 cm being omitted because of the web size itself.

Because measuring coordinates for non-stationary objects is impossible, spatial patterns of Aphididae and Diptera prey that was potentially available for web-building spiders were estimated using a 2 x 2-m grid of 16 regularly spaced sticky traps. Each trap consisted of 8 x 8-cm pieces of wire mesh coated with an insect banding compound (Tanglefoot Company, Grand Rapids, MI). Three grids were randomly located along a 150-m transect 30 m from the edge of the alfalfa field during each two-day web-survey period, with grid positions being used only once. Traps were collected and aphids and flies were counted under a stereomicroscope. Software for spatial analysis by distance indices (SADIE) was used to analyze the spatial pattern in the form of ranked count data (for details see Perry 1998). SADIE techniques have been used wisely to study predator and pest

distributions at larger scales (Ferguson et al. 2000, 2003, Warner et al. 2003, Winder et al. 2005). As those studies rely on trap capture data, results depend on the chosen trap distance (predefined scale) and only provide information about patterns at that scale.

Non-spatial Statistics

Spider web density and vegetation-height data were $\log_{10}$ transformed to approximate homogeneity of variance (after transformation, Levene test web-density: F=1.497, df=4,17; P=0.247; vegetation height: F=2.413; df=4,17; P=0.089) and analyzed performing a one-way ANOVA. LSD post-hoc tests were performed to test for differences between factor levels if the ANOVA was significant. Lycosid activity densities, which did not satisfy the assumption of homogeneous variances, were analyzed by Kruskal-Wallis ANOVA with subsequent multiple comparisons of ranks. Spider recolonization and plant growth rates after cutting were calculated from the difference between the spider density or vegetation height within each grid at a specific date compared to the average of the preliminary date divided by the number of days between those dates. The relationship between both variables was estimated by calculating the Spearman rank order correlation coefficient. Statistical analyses were performed with Statistica 7.1 (StatSoft Inc., Tulsa). Means are given ± one standard error, medians are shown with inter-quartiles.

4.4. RESULTS

Prey and Vegetation

Aphid prey availability differed between dates (F=3.86; df=4,10; P=0.038) with significantly more aphids being trapped per sticky trap grid before cutting, compared to 4 days after cutting (Fig. 4.2.a; LSD, P<0.001).

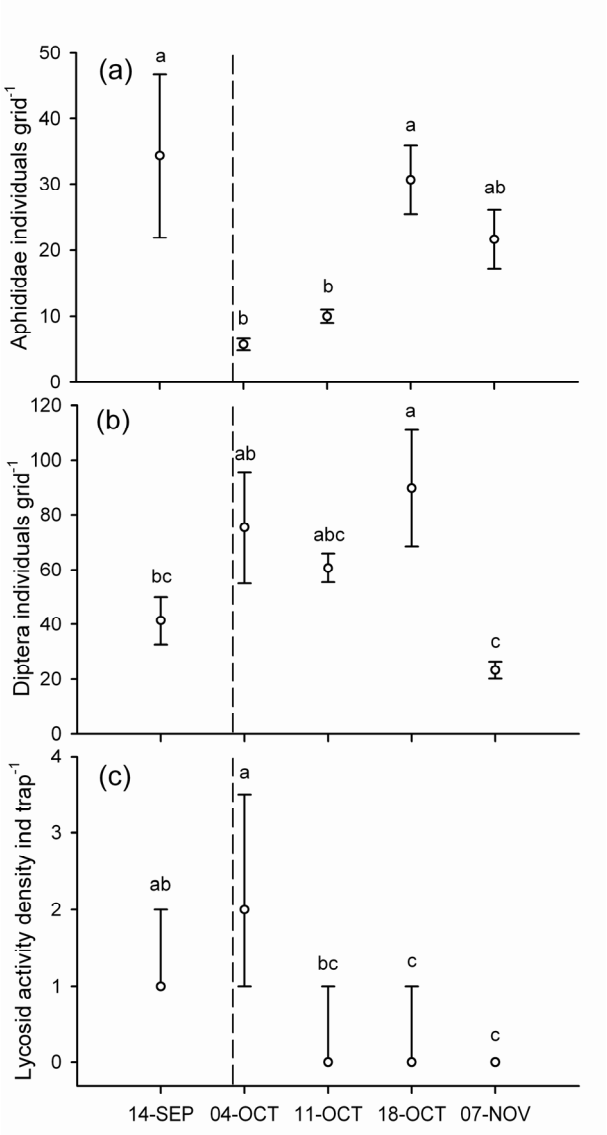

Figure 4.2. Aphididae (a) and Diptera (b) individuals per sticky trap grid (Mean ± SE) and wolf spider (c) activity-density (Median ± inter-quartiles) on each survey date. Different letters indicate significant differences between dates (a&b: LSD; c: Multiple Comparisons of Ranks). The dotted line shows the cutting date on 1 October.

Availability of aphid prey had recovered to pre-cutting levels at 18 October (LSD, P=0.692). Aphid prey was aggregated before cutting, but was randomly distributed at the analyzed scale thereafter. Before cutting, two trap grids had an index of aggregation (I_a) that indicated significant deviation from randomness, with aphid prey in the third replicate still tending towards aggregation (Table 4.1.).

Table 4.1. Estimated aphid prey availability (N), SADIE index of aggregation (I_a) and probability for a significant deviation of the distribution of available prey from spatial randomness in three grids of sticky traps.

	14 Sep			18 Oct			7 Nov		
Grid #	N*	I_a#	P	N*	I_a#	P	N*	I_a#	P
1	13	1.423	0.017	39	0.856	0.781	20	0.759	0.956
2	56	1.359	0.022	32	0.950	0.559	15	0.989	0.466
3	34	1.246	0.078	21	0.824	0.894	30	0.966	0.519

* individuals per trap grid (4 x 4 sticky traps; trap distance = 66 cm)

$I_a > 1$ indicates aggregation, $I_a < 1$ indicates regularity.

None of the sticky-trap grids indicated an aggregated availability of aphid prey at any date after cutting. Diptera prey availability also differed between daters (F=3.56; df=4,10; P=0.047) indicating highest availability two weeks after cutting (Fig. 4.2.b) and aggregation in some locations of one trap grid before cutting (N=96, I_a=1.465, P=0.010). Prey availability of Diptera did not deviate significantly from spatial randomness at all other dates (Table 4.2.).

Table 4.2. Distribution of spider webs in alfalfa plots and differences in predator, prey and plant characteristics at five sampling dates. The vertical line indicates date of cutting (1 Oct).

	14 Sep	04 Oct	11 Oct	18 Oct	07 Nov
Small scale web distribution	Regular	-	Regular	Random	Random
Aphididae distribution	Aggregated	-	Random	Random	Random
Diptera distribution	Aggregated/Random	-	Random	Random	Random
Web density	a	d	c	c	b
Lycosid activity density	ab	a	bc	c	c
Vegetation height	a	d	c	bc	b
Web recolonization rate	-	-	a	b	b
Plant growth rate	-	-	a	b	b

Different letters indicate significant differences with the letter "a" as highest and the letter "d" as lowest mean within each variable (see Material and Methods for statistical tests).

Vegetation height differed between dates (F=71.44; df=4,17; P<0.001) with alfalfa plants being higher before cutting and not recovering to pre-harvest heights after 35 days (Fig. 4.3.a; LSD, P<0.001). Plant growth rates were highest in the ten days after cutting, with significantly slower growth later on (Fig. 4.3.b; LSD, P<0.001).

Spiders

Web densities differed between most of the analyzed dates (Fig. 4.3.c; F=81.93; df=4,17; P<0.001).

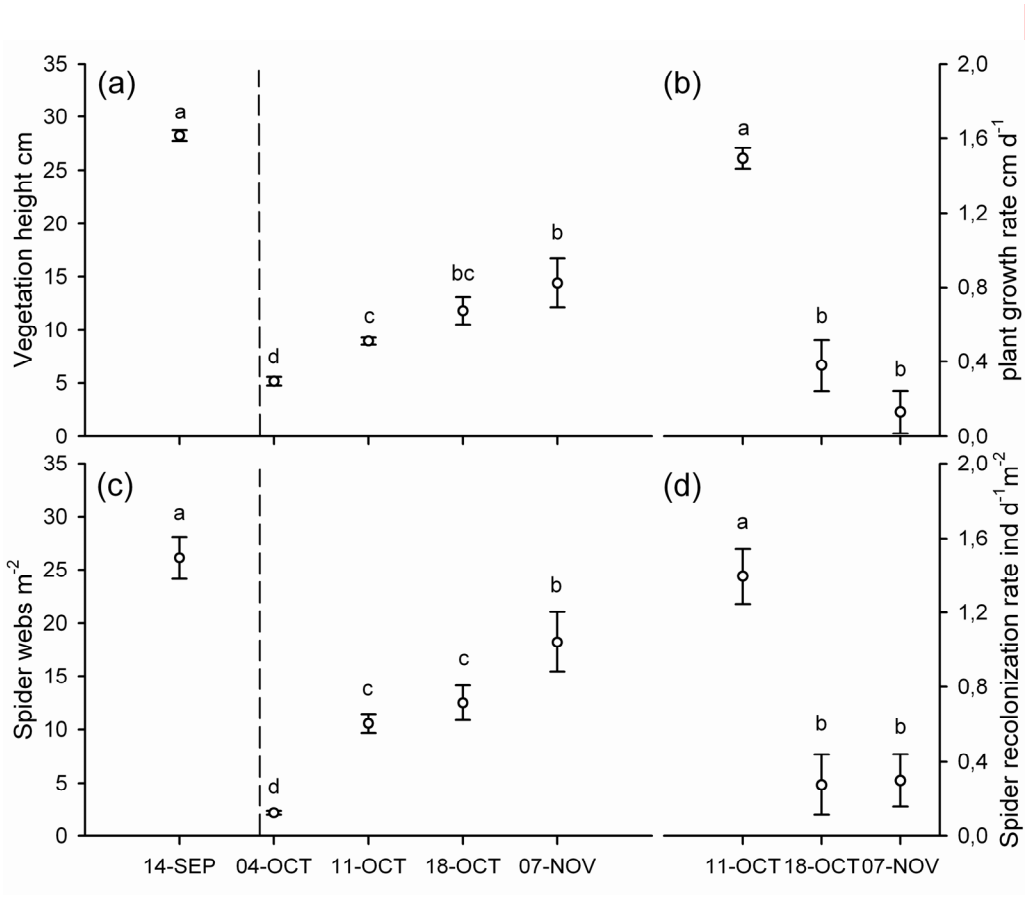

Figure 4.3. Vegetation height (a), plant growth rate after cutting (b), density of spider webs (c) and spider recolonization rate (d) after cutting (Mean ± SE) on each survey date. Different letters indicate significant differences between dates (LSD). The dotted line shows the cutting date on 1 October.

Cutting caused a significant decline with significantly higher web densities one week later (LSD, P<0.001), remaining at about this density after two weeks. Web density did not recover to pre-harvest levels 35 days after cutting (LSD, P=0.025). Spider recolonization rate differed between dates (F=45.33; df=2,9; P<0.001) being significantly higher during the two weeks after cutting than a week later (Fig. 4.3.d; LSD, P<0.001) or in November (LSD, P<0.001). Plant growth and spider recolonization rates were positively correlated (N=12, r_s=0.87, P<0.001). Wolf spider activity-density differed significantly with maximum activity-densities before and immediately after cutting (Kruskal-Wallis ANOVA; H=45.11; N=90; P<0.001; Fig. 4.2.c). Pitfall catches declined significantly between

4 and 11 October (Multiple Comparisons of Ranks, P=0.005) and did not recover to pre-harvest densities (Multiple Comparisons of Ranks, P=0.001).

The univariate spatial analysis of all recorded web locations independent of web-owner size indicated regularity at small distances before cutting and 11 days after cutting (Figs. 4.4.a-b).

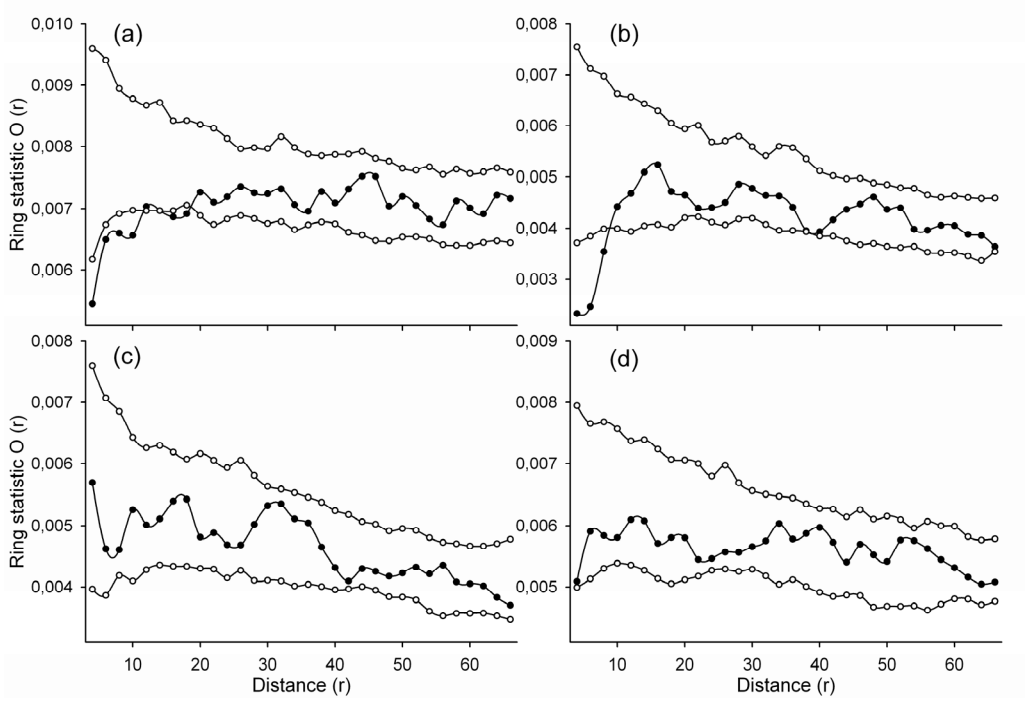

Figure 4.4. Univariate O-ring statistic (solid circles) analyzing the spatial pattern of all spider webs up to distances of 66 cm. 95% Confidence envelopes (open circles) are calculated by simulations of a heterogeneous Poisson process based on the intensity of the observed pattern. O-ring statistic crossing these envelopes indicate significant deviation from spatial randomness, with values below the lower envelope indicating spatial regularity and values above the upper envelope showing aggregation. N = the number of replicated 4-m² plots analyzed on each date

(a) 14 September (N=5)

(b) 11 October (N=4)

(c) 18 October (N=4)

(d) 7 November (N=4)

Web owners had significantly fewer neighbors than expected under the null model of a heterogeneous Poisson process at distances up to 18 cm before cutting, respectively up to distances of 8 cm eleven days after cutting. The distribution did not deviate from spatial randomness during later survey dates (Figs. 4.4.c-d). A bivariate analysis using a null model with larger species (> 5 mm: *F. coccinea, T. laboriosa and G. heptagon*) as fixed locations and randomly simulating smaller species

web locations (< 3 mm: *T. formica, E. autumnalis, M. unimaculata* and *G. foxi*) around those points, indicated repulsion of smaller web-owners through larger individuals at most web distances up to 32 cm (Fig. 4.5.).

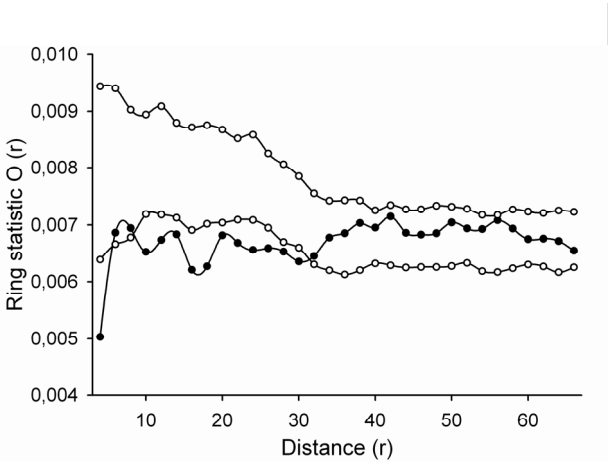

Figure 4.5. Bivariate O-ring statistic (solid circles) analyzing the spatial pattern of all spider webs up to distances of 66 cm on 14 September testing for the bivariate null model of independence between two patterns. Pattern one (large species > 5 cm) is set as fixed, while the null model assumes a random distribution of pattern two (small species < 3 cm). 95% Confidence envelopes (open circles) are calculated from simulations of a heterogeneous Poisson process based on the intensity of both patterns in each grid. O-ring statistic crossing these envelopes indicate significant deviation from spatial randomness, with values below the lower envelope showing repulsion of smaller individuals through larger neighbors and values above the upper envelope showing attraction between the two size classes.

4.5. DISCUSSION

Effects of prey and management on spider web spatial patterns

Aphid prey availability was higher in some locations within grids than in others before cutting, probably as a consequence of their dispersal behavior and parthenogenetic reproduction (Dixon 1998, Östman 2002). We did not find aggregation of web locations at the same scale at which aphid prey was found to occur in clusters. This absence of a connection between the smalls scale spatial availability of aphid prey and spider web distribution differs from the finding of Harwood *et al.* (2003) that web-building spiders were spatially associated with prey in wheat fields. Web builders in our study showed no aggregation at any analyzed date or scale. If web-builders in our alfalfa field were spatially associated with prey over the range of scales analyzed, than those prey taxa do not aggregate at small scales. A recent molecular study indicates a strong feeding link between decomposer prey

(Collembola) and web builders (Linyphiidae) (Agusti et al. 2003). Collembola may be of higher food quality than aphids, which are poor-quality prey for several spider species (Toft 2005). Although it is possible that webs in our alfalfa field were associated with non-aggregated prey from the decomposer subsystem, several studies indicate that mites and springtails aggregate at small scales in response to microhabitat heterogeneity (Rebek et al. 2002, Harwood et al. 2003, Ducarme and Lebrun 2004, Gear and Schmitz 2005).

Absence of evidence for small scale spatial association between predator and prey in our study is in line with results from a large scale spatial analysis (SADIE) on cursorial-predator distribution in alfalfa and soybean agroecosystems by Pearce and Zalucki (2006), who found no association between surface- and foliage-dwelling predators and prey at the analyzed scale. We suggest that agroecosystems such as alfalfa, which exhibit high plant coverage and a relatively uniform micro-climate, differ from crops with regular seed stands by not showing intense prey aggregations in distinct patches. Microhabitats that are favorable in terms of climate and vegetation structure are distributed more randomly in alfalfa than in wheat fields, in which high-quality microhabitats display a regular dispersion pattern (Harwood et al. 2001a).

Cutting reduced web-building spider abundance, but had no immediate impact on the spatial distribution of webs. In contrast to results from some other studies (Howell and Pienkowski 1971, Thomas and Jepson 1997), web-building spider numbers did not recover from cutting. This reflects the finding by Bell et al. (2002b) that the date of cutting determines the time necessary for recovery. Our study was carried out in the end of the growing season, when temperatures are declining and after the main peaks of spider abundance in spring and late summer (Culin and Yeargan 1983a, 1983b). Wolf spiders had the highest activity-density after cutting, possibly reflecting elevated activity in response to reduced vegetation coverage. Langellotto and Denno (2006) documented that habitat complexity reduced rates of intraspecific antagonistic interaction and cannibalism in a wolf spider species. Our result of small scale regularity after cutting support the assumption that reduced habitat complexity in response to cutting could contribute to increased rates of intraguild interactions.

Effects of intraguild interactions on spider web spatial patterns

Webs were more regularly spaced at small distances than expected under the null model of a random pattern in times of high web-spider abundance, during and immediately after highest wolf-spider activity-abundance, and when re-colonization rates of web-building spiders were highest. Plant growth and web-building spider recolonization rates were positively correlated, but regular distributions of web locations were only observed at dates with the most contrasting differences in plant characteristics. Our spatial analysis showed no deviation from randomness later in the season, when web density and vegetation height became more similar between survey dates (Table 4.2.). We therefore suggest that small scale spatial regularity is not a feature caused by distinct vegetation characteristics. Even though we cannot completely rule out an impact of environmental heterogeneity, we minimized any such effect by using an appropriate null model for web location analysis. As we could not find any small scale aggregation in response to clusters of high prey availability and because we utilized a null model that incorporated environmental heterogeneity for spider web analysis, we propose that small-scale regularity in web dispersion resulted from two types of intraguild interactions (i.e. intra- and inter-specific interactions within a "guild" of generalist predators -- as some webs were vacant, species determination was not always possible in our study, we can therefore not distinguish inter- from intra-specific interactions). First, individuals searching for web sites might perceive other established spiders and actively avoid building webs nearby (spatial avoidance). Hodge and Storfer-Isser (1997) reported aggregation of nearest neighbors in two web-building species and suggested silk-mediated attraction between individuals as the cause (conspecific cuing). Spatial avoidance assumes that web-site searching individuals perceive other webs and in contrast to the findings of Hodge and Storfer-Isser (1997), may avoid building their own webs nearby. This avoidance behavior may be advantageous as it could reduce competition and enhance prey availability for web-owners. This assumption is supported by Spiller (1986) for two web-building spider species, indicating that removal of one species improved prey availability for the second species.

Secondly, direct encounters between spiders, including web-builders and wolf spiders, could result in the observed regularity before and after cutting. The assumption that intraguild interactions caused spatial regularity is supported by the observation that larger web owners had fewer smaller neighbors

than expected under spatial randomness at radii up to 32 cm around their webs. Larger web-building linyphiids have a competitive advantage over smaller neighbors (e.g. Harwood et al. 2001a). From our spatial analysis we cannot determine if the observed small-scale regularity is a consequence of predation or simply repulsion. A mesocosm experiment showed that heterospecific web-building linyphiids from alfalfa fields preyed more frequently on spiders under increasing spider density (Harwood and Obrycki 2005). Such intraguild predation in web-building spiders is probably limited to species that forage in excess of their webs (Wise 2006). Our spider community includes some of the species studied by Harwood and Obrycki (2005) and was dominated by linyphiids (67% of all adults), which are known to forage in excess of their webs (Alderweireldt 1994b); therefore, we suggest that spatial regularity at least in part developed though intraguild predation. Denno et al. (2004) documented such intraguild predation through lycosids feeding on a small sheet-web weaving species (Linyphiidae). In our study spider webs showed small scale regularity only in times of highest wolf spider activity density, indicating that lycosids influenced pattern formation. Interference competition (repulsion) is another possible explanation for the effect of direct encounters on spatial pattern development. Competition between spiders should be more intense in agroecosystems as compared to natural ecosystems (Marshall and Rypstra 1999). Samu et al. (1996) increased the density of webs occupied by a linyphiid species by artificially enhancing the number of web sites in a wheat field. The investigators found indications of interference competition for webs at high densities, but also documented tolerance between neighbors in areas with enhanced numbers of artificial web sites.

Our small scale approach for spatial analysis over multiple scales demonstrates the differences to large scale studies at a pre-defined scale. Harwood et al. (2001a) point out the importance of small-scale analysis of web-building spider distribution, a recommendation supported by our results. Spatial analysis using grid-based count data on a single, larger scale would have overlooked small-scale regularity if the predefined spatial resolution (grid size) would have been too coarse. Whereas simple dispersion indices often only incorporate a single measure of nearest neighbor distance (Clark and Evans 1954) and therefore do not include information about the relationship between points at smaller or larger distances. We suggest that the paucity of documented regular dispersion patterns for web-

building spiders might at least in part come from the use of spatial analysis techniques not focusing on multiple scales.

Conclusions

This study suggests that intraguild interactions contribute more than prey-mediated aggregation to small scale web-dispersion patterns of spiders in alfalfa. We documented regularity at small distances for spider webs with no spatial distribution reflecting the clustered occurrence of available prey. Cutting of alfalfa did not directly influence web distribution, as webs showed regularity before, and a week after cutting. Nevertheless, small-scale regularity disappeared as web densities recovered in the weeks after cutting, an observation deserving future investigation. Analyzing pattern development over a range of spatial scales in addition to knowledge of factors affecting overall web-spider density is crucial for further refinement of conservation biological control strategies involving web-building spiders. Knowledge of spatial needs at large and small scales and the development of measures to minimize intraguild interactions may allow maximizing predator survival and efficiency for pest control (Provencher and Vickery 1988, Scheu 2001).

Chapter 5 - Effects of prey from the detrital food web and habitat complexity on generalist predator numbers and herbivore suppression

5.1. ABSTRACT

The effectiveness of generalist predators as biocontrol agents is influenced by the presence of non-pest prey from the decomposer and herbivore subsystems, and structural complexity of the habitat. Organic farming supports decomposer populations, and also enhances habitat complexity due to increased weed density and diversity. In a replicated field experiment, we manipulated the availability of prey from the decomposer subsystem and the vegetational structural complexity in a winter wheat field, in order to simulate conditions characteristic of organically managed cereal fields. We then analyzed the impact of our microhabitat manipulations on densities of major generalist predators, decomposers and herbivore pests. Isotomid Collembola responded as predicted to the manipulations of the detrital food web, with lowest activity-densities (AD) in plots treated with a soil insecticide (reduced) and gradually increasing AD in untreated plots (control) and plots receiving a detrital subsidy (enhanced). Aphid density mirrored that pattern, with aphids apparently benefiting from a release from predation due to more abundant alternative prey from the decomposer subsystem. Carabid beetles and cursorial spiders preferred less structurally complex plots, whereas the AD of entomobryid Collembola was lowest in these plots. This inverse pattern likely was a consequence of increased predation on Collembola, or a change in Collembola behavior, in the less-complex treatment. Addition of organic matter and restricted herbicide applications in organically managed agroecosystems cause favorable conditions for generalist predators. However, preferences for decomposer prey may reduce the potential of certain generalist predator groups for aphid control. Furthermore, enhanced structural complexity alone might not improve aphid suppression, leading one to predict that any positive effect of weeds on carabids and cursorial spiders is likely due to indirect effects mediated through effects of weeds on densities of non-pest prey.

5.2. INTRODUCTION

Prey switching between non-pest (alternative prey) and pest (target prey) species, and stability of predator populations, are two important conditions for pest suppression by generalist predators (Scheu 2001). Features that support generalist predator populations in agroecosystems are an abundant soil fauna and the presence of weeds. Both characteristics are typically fostered by organic farming (Bengtsson et al. 2005).

Increased prey availability from the decomposer subsystem may stabilize generalist predator populations in times of limited herbivore prey availability (Settle et al. 1996; Wise et al. 1999). Fast recolonization of agroecosystems by generalist predators and increased survival rates favored by decomposer prey have been suggested to significantly contribute to successful pest management in field crops (Scheu 2001). Such enhancements of generalist predator densities by subsidies from the decomposer subsystem have been documented in rice (Settle et al. 1996) and vegetable garden systems (Halaj and Wise 2002).

Overlapping density peaks of decomposer and herbivore populations, however, may reduce biocontrol by generalist predators. The impact of generalist predators on pest densities is limited if they fail to switch to pest prey; consequently, prey from the decomposer subsystem might also decrease the biocontrol effectiveness of a generalist predator (Sunderland and Samu 2000). Two scenarios are likely under which generalist predators do not switch to pest prey species. First, toxicity or unpalatability of pest prey species may prevent switching. Reviewing the available data on the food quality of aphids for generalist predators, Toft (2005) stressed that aphids are of limited quality and several generalist predator species even developed an aversion against such prey. The second scenario is based on optimal foraging theory, in which prey preference depends not only on prey availability but also on search and handling time (Pyke 1984). Many generalist predator species in arable land are surface-active hunters and forage little in the vegetation layer. Their potential for pest suppression might therefore be limited, even if surface-based prey is rare. The assumption of predators switching between non-pest and pest prey in response to density changes therefore still is questionable. As organic matter forms the basis of the decomposer system, the impact of organic matter addition on the

performance of generalist predators and pest suppression in agroecosystems needs to be investigated in more detail (Sunderland and Samu 2000).

Reviews on consequences of habitat structure on natural enemies generally conclude that an increase in habitat complexity is associated with increased predator density (Uetz 1991; Wise 1993) and therefore potentially enhances herbivore suppression (Landis et al. 2000). Recent reviews have called for an experimental and mechanistically orientated analysis of the impact of habitat complexity on natural enemies in order to uncouple links between structure and prey resources (Rypstra et al. 1999; Sunderland and Samu 2000; Langelloto and Denno 2004). The majority of manipulative studies analyzing the impact of habitat-structure alterations and their consequences for generalist predators focused on non-agricultural systems (e.g. McNett and Rypstra 2000), emphasizing the need for comparable experiments in agroecosystems (Sunderland and Samu 2000). Such experiments are important, as enhancing structural complexity may not always result in increased predator abundance. Spiders for example have been shown to respond positively (Robinson 1981; Samu et al. 1996; Bell et al. 2002b), not at all (Riechert 1990; Samu et al. 1999) or even negatively (Scheidler 1990; De Souza and Martins 2005) to increased structural habitat complexity. This pattern is also true for carabid beetles, with several species preferring open, less vegetation-covered microhabitats (Holland 2002). Beneficial effects of weeds on generalist predators are caused by different mechanisms. Pollen and seeds of weeds may function as supplementary food (Norris and Kogan 2005), weeds may attract alternative prey species (Weyman et al. 1995), weeds may cause a more favorable microclimate (Alderweireldt 1994a), weeds may function as refuges from management practices and predation (Finke and Denno 2006), and weeds may function as additional web-attachment sites for web-building spiders (McNett and Rypstra 2000). Predicting effects on pest suppression under changes of habitat structure is of particular importance since weeds often detrimentally affect crop yield (Wyss et al. 1995; Wyss 1996).

Weeds, therefore, may enhance generalist predator numbers through attraction of additional prey and/or through the alteration of structural complexity. Though these two mechanisms are not mutually exclusive, their consequences differ for the potential of generalist predators to limit pests. Increased densities of generalist predators resulting from additional herbivore prey in weedier arable fields might

not necessarily enhance pest suppression rates if predators switch from pests to abundant and potentially more nutritious weed-based herbivore species (Kemp and Barrett 1989). In contrast, pest suppression should be significantly enhanced if structural complexity alone contributes to increased generalist predator activity and abundance.

The present study investigated three major questions. (1) Does increased prey availability from the decomposer subsystem increase the effectiveness of generalist predators in controlling pest species (prey availability treatment)? (2) Does increased structural complexity increase the degree to which generalist predators suppress pest populations (structural complexity treatment)? (3) To what extent do habitat features and the availability of alternative prey interact to modify pest suppression through generalist predators?

5.3. MATERIAL AND METHODS

Study site and taxonomic groups

Between May 26 and 28, 2005 we established 48 plots along the edge of a winter wheat field at the experimental farm "Reinshof" located close to Göttingen (Lower Saxony, Germany). The soil is a loamy flood plain soil formed by clayey silt (pH 7.5; for more information see Albers et al 2006). The fields were under conventional management with no insecticides applied prior to the end of the experiment. The open experimental plots of 2.25 m² were established 4 m apart in eight blocks, with 8 m between blocks and 5 m to the edge of the field.

A wheat field was chosen as the model system because feeding links of herbivores and predators in wheat fields are well documented, and results are assumed to hold for a large number of temperate cereal agroecosystems. Analyzed taxa include generally abundant co-occurring organisms from the decomposer subsystem (isotomid and entomobryid Collembola) and economically important herbivores (aphids). The analyzed generalist predator taxa (Araneae, Carabidae and Staphylinidae) are known to attack prey in both subsystems, with some species being specialized on one trophic level (e.g. *Loricera pillicornis*, Carabidae: Collembola, Hintzpeter and Bauer 1986; *Tachyporus hypnorum*, Staphylinidae: aphids, Dennis et al. 1990).

Experimental design

In a 2x3 complete factorial design we manipulated structural complexity by first manually removing weeds from all plots and then adding five plastic plants in a standardized arrangement (Fig. 5.1.) to a randomly chosen half of the plots in each block (structurally complex).

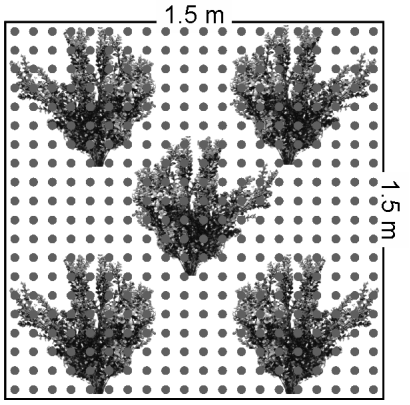

Figure 5.1. Structural complexity treatment showing the standardized arrangement of plastic plants between rows of wheat stands in 2.25-m² experimental plots.

Plastic plants (Flora-Seta GmbH, Nürtingen, Germany) were 30 cm high and had between 12 and 14 branches covering a surface radius of approximately 20 cm per plant. The other half of the experimental plots remained untreated (structurally simple). Structurally simple plots were established to simulate wheat fields under conventional management and reduced weed coverage, whereas structurally complex plots resemble vegetation complexity in organically managed fields without providing further attributes of living weeds.

As a second factor we manipulated prey availability from the decomposer subsystem by either applying oat flake flour (1 kg/plot, enhanced density) or by hand-spraying chlorpyrifos (5 g/m²; Hortex, Scotts Celaflor, Salzburg, Austria; reduced density) to the soil surface, respectively. One third of the plots were untreated (control). Chlorpyrifos is an organophosphate that is applied as soil insecticide with strong and long-lasting effects on Collembola abundance (Frampton 1997, 2000; Endlweber et al. 2006). Lethal effects on surface-active predators are weak (Curtis and Horne 1995; Filho et al. 2002). Wang et al. (2001) observed no negative effects of chlorpyrifos application on soil-based predators (Carabidae, Staphylinidae and Lycosidae). Only plant-inhabiting predators were negatively influenced by chlorpyrifos, an observation also supported for vegetation-based linyphiid

spiders by Frampton (1999). We applied the insecticide directly to the soil surface with no contact to the vegetation to minimize effects on vegetation-based Arthropods. Direct effects on mobile, surface-active arthropods were further reduced by restricting the application in space and time (38 d before sampling). Vegetation cover and plant species richness are not influenced by chlorpyrifos (Schädler et al. 2004); therefore, chlorpyrifos qualifies as a valid tool to specifically target soil fauna abundance (Endlweber et al. 2006).

Detrital subsidies in the form of a mix of chopped mushrooms, chopped potatoes and *Drosophila* instant medium, or a mix of wheat straw and horse manure, have been successfully used to enhance Collembola densities in vegetable gardens and forests (Chen and Wise 1999; Halaj and Wise 2002). The oat flake flour used in this study was assumed to either improve food availability for decomposers directly or indirectly by enhancing fungal growth.

Data collection

From July 2 the centre of each experimental plot was sampled for two weeks with a single pitfall trap (distilled water with detergent in glass cups 14 cm deep and 8 cm in diameter). Afterwards the 1.3 m² central area of each plot was fenced with a plastic barrier (50 cm high) and suction sampled under dry weather conditions for 2 min (EcoVac Insect suction sampler modified for sampling in wheat, EchoTech, Bonn, Germany). Sampling with unfenced pitfall traps estimates the activity-density (AD) of surface-active arthropods in the entire plot, whereas fenced suction sampling estimates the abundance (density) of vegetation-based taxa (Sutherland 1996).

Pitfall catches and suction samples were transferred to collection vials in the field and stored cool for transport. Ethyl acetate was added to the suction samples to prevent predation during transport. Pitfall samples were sieved in the laboratory (100 µm gauze) and stored in 70% ethanol. Dry suction samples were cleared from large debris using a dissection microscope and then transferred to 70% ethanol. These samples were later sieved (100 µm gauze) using a wash bottle and water to clean them from soil particles. All samples were analyzed in a petri dish by sorting and counting individuals at two magnifications (6.5x and 12.5x) using a stereoscope (Leica MZ12). Because aphids were abundant in

suction samples, individuals were only counted in 10 randomly chosen grid cells (10 cm²) per petri dish (95 cm²).

Determination of Collembola subfamilies followed a key by Zettel (1999) spider species were determined according to Heimer and Nentwig (1991). Classification of spider families to cursorial and web-building guilds followed Uetz et al. (1999) with the exception of Linyphiidae from the subfamily Erigoninae and *Pachygnatha degeeri* (Tetragnathidae), which were classified as cursorial hunters according to Alderweireldt (1994b), Thornhill (1983) and Harwood et al. (2005). Ground beetle (Carabidae) species and rove beetle (Staphylinidae) subfamilies were determined using keys by Freude et al. (1964, 1976). Average daily temperature was measured with a single temperature logger (TinyTag 2 Data Loggers, Chichester, UK) in three plots per structure treatment (within the ummanipulated decomposer prey treatment), either located under natural or artificial vegetation. Another three loggers were placed in open areas between wheat stands in three plots of the structurally simple treatment.

Data analysis

All AD and abundance data were $\log_{10}(x+1)$ transformed to improve homogeneity of variance. A two-way (2x3) multivariate analysis of variance was performed with cursorial spider, ground beetle, rove beetle, isotomid and entomobryid Collembola AD, aphid and web-building spider abundance as dependent variables. Structural complexity (simple and complex) and prey availability from the decomposer subsystem (reduced, enhanced and control) were the fixed independent variables. We used Pillai's criterion to test for significance of main effects and interactions as it is most robust against violations in terms of homoscedasticity and normal distribution (Scheiner and Gurevitch 2001). Entomobryid and ground-dwelling predator AD were correlated using a Spearman rank correlation.

We conducted a second MANOVA in order to identify treatment effects on the common taxa within these more inclusive taxonomic/guild categories. The most abundant cursorial (*Erigone* sp., *Erigone atra* and *Erigone dentipalpis*: females were not distinguished) and web-building (*Tenuiphantes tenuis*, *Bathyphantes gracilis* and *Meioneta rurestris*) spider species, and predatory

beetle taxa (Staphylinidae: Aleocharinae and Staphylininae; Carabidae: *Loricera pillicornis*), were analyzed as the dependent variables within a 2x3 MANOVA. Taxa were defined as common if they were found in > 24 plots with a minimum average abundance of one individual per plot. In case of a significant MANOVA main effect, we performed a protected one-way ANOVA for each species or subfamily. We compared differences between treatments for single dependent variables using contrast statements rather than multiple tests, as recommended by Quinn and Keough (2002).Statistical analyses were calculated using Statistica 7.1. (StatSoft, Hamburg, Germany).

5.4. RESULTS

Average daily air temperature under natural and artificial vegetation did differ by 0.3° C (contrast analysis, P=0.287), but surface temperature was 1.0° C higher in open, uncovered patches than under wheat or artificial vegetation (contrast analysis, P=0.040). Prey ($F_{(14,74)}$=4.34, P<0.001) and structure ($F_{(7,36)}$=2.29, P=0.049) significantly influenced the dependent variables; the interaction term was not significant ($F_{(14,74)}$=1.02, P=0.442). Predator species and subfamilies were also significantly influenced by prey ($F_{(14,74)}$=1.85, P=0.048) and structure ($F_{(7,36)}$=2.99, P=0.014), with no significant interaction term ($F_{(14,74)}$=0.844, P=0.620). We further analyzed the impact of each main factor on single variables by contrast analysis.

Decomposer-prey manipulations

Isotomid collembolans, the most abundant surface-active decomposer group analyzed, responded as predicted to decomposer-prey manipulations (Fig. 5.2.a).

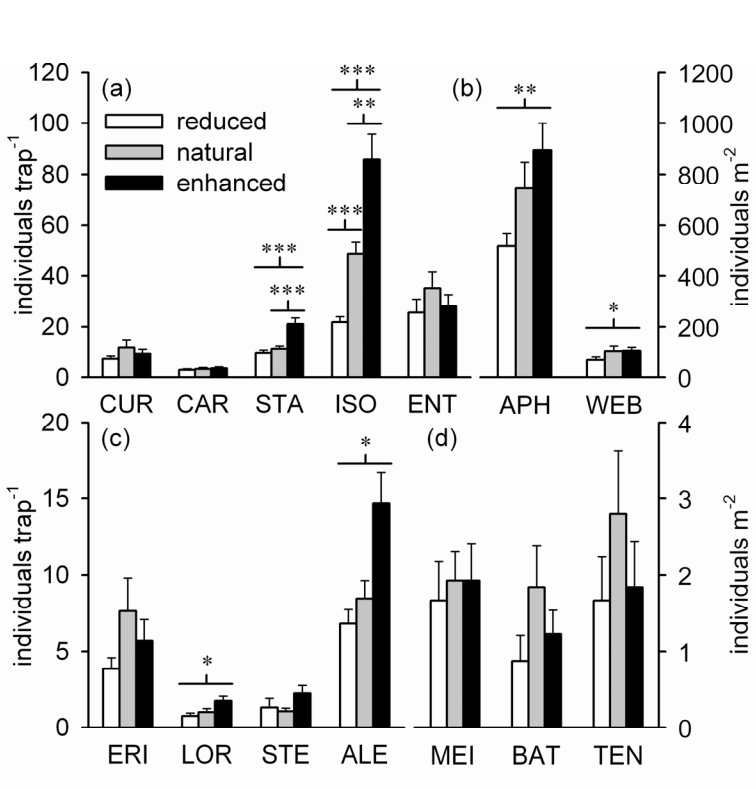

Figure 5.2. Number of individuals in pitfall traps (a) and suction samples (b), and number of individuals per common predatory species/subfamily in pitfall traps (c) and (d) suction samples in reduced, natural (control) and enhanced decomposer prey availability plots (mean ± SE). Asterisks denote significant differences as analyzed with contrast comparison: ∗: p<0.05, ∗∗: p<0.01, ∗∗∗: p<0.001. Short bars indicate a difference between the control (the intermediate treatment) and one of the two treatment extremes, long bars indicate that there were significant differences only between the two extreme treatments. ALE = Aleocharinae, APH = Aphididae, BAT = *Bathyphantes gracilis*, CAR = Carabidae, CUR = cursorial spiders, ENT = Entomobryidae, ERI = *Erigone* sp., ISO = Isotomidae, LOR = *Loricera pillicornis*, MEI = *Meioneta rurestris*, STA = Staphylinidae, STE = Staphylininae, TEN = *Tenuiphantes tenuis*, WEB = web-building spiders.

Activity-density was four times higher in the detrital subsidy treatment compared to the chlorpyrifos treatment (contrast analysis, $P<0.001$) and almost two times higher than the control treatment (contrast analysis, $P=0.001$). Rove beetle AD was 1.9x higher in the detrital-subsidy treatment than the control (contrast analysis, $P<0.001$), and 2.2x higher than the chlorpyrifos treatment (contrast analysis, $P<0.001$). Carabid beetles and cursorial spiders did not respond to increased AD of alternative prey. Aphid abundance was 1.7x higher in detrital-subsidy than chlorpyrifos plots (Fig 5.2.b; contrast

analysis, P=0.005), but aphid abundance in neither treatment differed significantly from the control. Web-building spiders were 1.5x more abundant in the detrital subsidy treatment compared to the chlorpyrifos treatment (contrast analysis, P=0.030), with no significant difference between these two treatments and the control.

Although prey availability did not affect overall carabid AD, the most common carabid species, *L. pillicornis,* responded to prey-density manipulations (ANOVA, $F_{(2,42)}$=3.84, P=0.029). This species AD was 2.3x higher in detrital-subsidy than chlorpyrifos-treated plots (Fig 5.2.c; contrast analysis, P=0.011), and was1.8x higher than the control (contrast analysis, P=0.052). Only the subfamily Aleocharinae showed a similar trend (ANOVA, $F_{(2,42)}$=3.21, P=0.051), with its AD being 2.2x higher in the detrital-subsidy than chlorpyrifos treatment (contrast analysis, P=0.018). None of the web-building spider species responded to prey-density manipulations (Fig 5.2.d), but immatures abundance was 1.6x higher under detrital subsidy as compared to the chlorpyrifos treatment (contrast analysis, P=0.026).

Structural complexity manipulation

Activity-density of cursorial spiders was 1.6x higher (contrast analysis, *P*=0.047) and AD of ground beetles was 1.5x higher (contrast analysis, *P*=0.022) in the open, structurally less-complex treatment (Fig. 5.3.a).

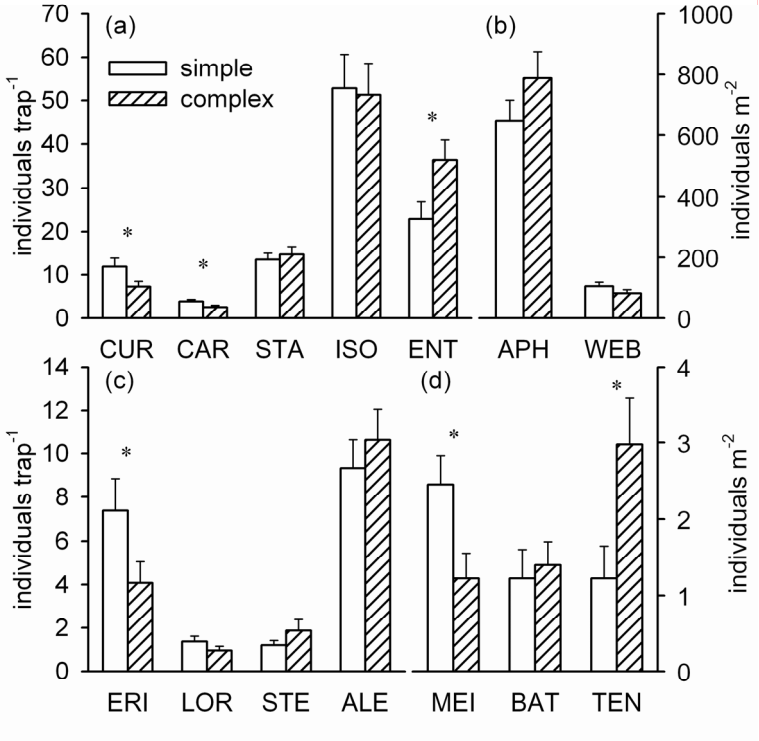

Figure 5.3. Number of individuals in pitfall traps (a) and suction samples (b), and number of individuals per common predatory species/subfamily in pitfall traps (c) and (d) suction samples in simple and structurally complex plots (mean ± SE). Asterisks denote significant differences as analyzed with contrast comparison: ∗: p<0.05, ∗∗: p<0.01, ∗∗∗: p<0.001. For abbreviations see Fig. 5.2.

Entomobryid collembolans, showed an inverse pattern; their AD was 1.6x higher in the structurally complex plots (contrast analysis, *P*=0.012). Activity-densities of surface-active predators and entomobryid Collembola were negatively correlated (N=48, r_s=-0.385, *P*=0.007). Aphids and web-building spiders showed no response to increasing structural complexity (Fig. 5.3.b).

Within the cursorial spiders, *Erigone* sp. was 1.8x more abundant in structurally simple plots (Fig. 5.3.c; $F_{(1,46)}$=5.25, *P*=0.027). The two most abundant web-builders showed contrasting patterns, with *T. tenuis* being 2.4x more abundant in structurally complex plots (Fig. 5.3.d, $F_{(1,46)}$=6.59, *P*=0.014) and *M. rurestris* being twice as abundant in structurally simple plots ($F_{(1,46)}$=6.52, *P*=0.014).

5.5. DISCUSSION

Prey availability

The assumption that dual-subsystem omnivory is of fundamental importance in terrestrial food webs (Polis and Strong 1996; Scheu 2001) may explain the increased interest in the role of prey quality (reviewed in Toft 2005) and prey type (reviewed in Symondson 2002) for generalist predators. We experimentally manipulated the AD of a major prey group from the decomposer subsystem in order to test the hypothesis that increased availability of alternative prey increases pest suppression (Harmon and Andow 2004). In line with earlier findings (Settle et al. 1996; Halaj and Wise 2002; Wise et al. 2006), we uncovered positive effects of increased decomposer AD on generalist predators.

Predator-mediated indirect effects of one prey type on another can be either positive or negative, with different consequences for the effect of enhanced alternative prey on the control of pest species (Holt 1977). Negative indirect effects, in which numbers of generalist predators increase in response to increased availability of "alternative" (non-pest) prey and consequently exert greater mortality and/or increase emigration of "target" (pest) prey, strengthen biological control. If, in contrast, an abundant non-target prey draws predator attention away from a target prey (positive indirect prey-prey interaction), predators would become less effective in pest control. In our field experiment, herbivore suppression was reduced by a factor of two under enhanced levels of alternative decomposer prey - a positive indirect prey-prey interaction.

A laboratory experiment simulating a simplified food chain illustrates a comparable negative effect of decomposer prey on pest suppression by generalist predators (Madsen et al. 2004). A wolf spider and a carabid beetle species significantly reduced aphid numbers in treatments without decomposer prey compared to microcosms with alternative prey (Collembola). Koss and co-authors studied prey-prey interactions in potato fields, with either Colorado potato beetles (CPB; Koss et al. 2004) or aphids (Koss and Snyder 2005) as alternative herbivore prey for predatory bugs. Results of a microcosm experiment defining aphids as target and CPB eggs as alternative prey did not reveal reduced predation on aphids in the presence of alternative prey (Koss et al. 2004). In contrast, increased availability of aphids, now defined as alternative prey, reduced predation rates on the Colorado potato beetle in field and laboratory experiments (Koss and Snyder 2005). Predatory bugs

presumably switched from predation on abundant Colorado potato beetles early in the growing season to increasingly available aphid prey later in the season. Halaj and Wise (2002) did not find consistent effects of experimentally increased decomposer prey availability on herbivore control in a cucumber and squash garden systems. Lack of an effect was mainly attributed to the low abundance of pests in squash and the unusually high densities of pests in cucumber. The absence of evidence for switching from decomposer prey to herbivore pests by a dominant, large wolf spider species in cucumber gardens suggests that enhanced densities of decomposer prey, which lead to increased wolf spider abundance, could cause increased pest suppression (Wise et al. 2006).

We identified a strong positive prey-prey interaction within a manipulative field experiment, defining alternative prey as non-pest prey. In contrast to the above- mentioned herbivore-herbivore systems (Koss et al. 2004; Koss and Snyder 2005), knowledge about decomposer-herbivore interactions might have even stronger implications for improving conservation biological control in sustainable farming systems. Farming practices such as low-tillage, mulching or the addition of organic matter (farmyard manure) are potentially beneficial for decomposer animals (Bengtsson et al. 2005; Thorbek and Bilde 2004). Therefore, identifying predator-mediated decomposer-herbivore interactions has consequences for pest suppression and the improvement of conservation biological control. Given the fact that the AD of two surface-active predator taxa (Carabidae and cursorial spiders) remained constant irrespective of isotomid density, our data suggests reduced predation on aphids if the availability of prey from the decomposer subsystem increases (Fig. 5.4.a).

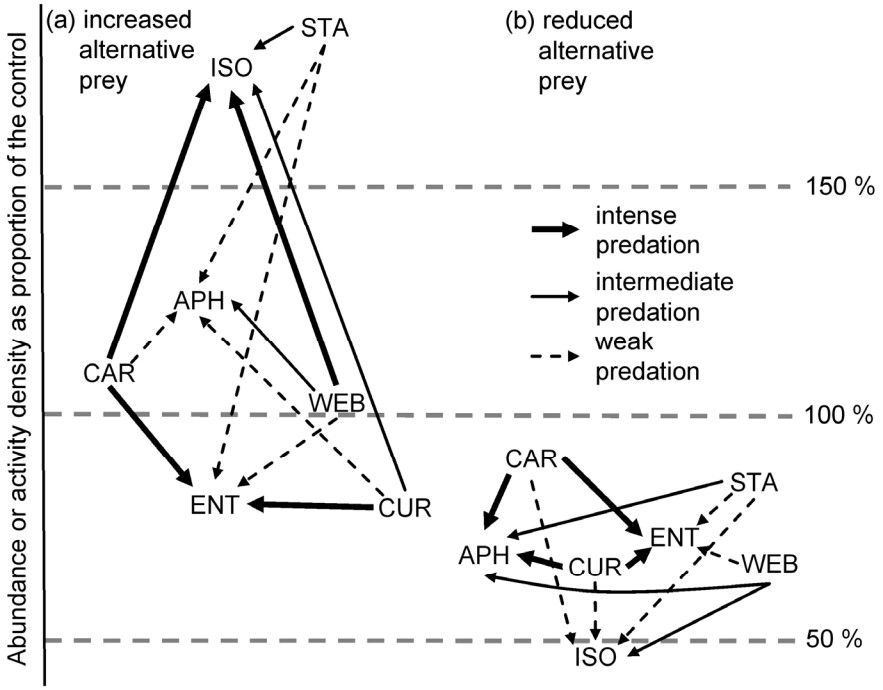

Figure 5.4. Predation intensity under (a) high and (b) low availability of alternative decomposer prey. The vertical position of each taxon represents the relative abundance or activity-density (AD) as a proportion of the control treatment. Dotted horizontal lines therefore correspond to each group's total abundance or AD in the control treatment. For abbreviations see Fig. 5.2.

This result is supported by molecular studies showing negative effects of high Collembola availability on aphid predation by certain web-building spiders (Harwood et al. 2004). In our experiment, applying insecticide to the soil did not indirectly affect aphid abundance (comparing decreased prey-availability plots with control plots); in contrast, aphid densities were two times higher in enhanced decomposer-prey plots compared to the soil-insecticide treatment. We attribute the positive indirect effect of increasing alternative-prey availability on aphid abundance to switching by generalist predators from pests (aphids) to decomposer prey (Collembola) (Fig. 5.4.b).

Using stable isotopes, McNabb et al. (2001) uncovered a strong link between small spiders (linyphiids and immature lycosids) and decomposer prey, with larger spiders more likely feeding on herbivore prey. The two carabid species in their study differed in isotope signature, reflecting the diverse species-specific feeding behavior of carabid beetles. Wise et al. (2006) showed that carbon-isotope signatures of small wolf-spider species and the juvenile stages of large species mirrored signatures of Collembola in both control and detritus-addition plots. Adults of one large species appeared to shift to detrital prey in plots with experimentally enhanced decomposer prey, although

large standard errors make the results equivocal. In contrast, adults of another lycosid species clearly continued to feed in the herbivore-based web even when prey in the detrital web increased in abundance. In these experiments the pests were not aphids, but were cucumber beetles and squash bugs. Our results suggest a contrary scenario, in which increased detrital prey led to decreased predation on aphid pests.

In our experiment, carabids and cursorial spiders did not show a numerical response to enhanced decomposer prey levels, in contrast to increased numbers caused by detrital supplements in earlier experiments (Halaj and Wise 2002; Wise et al. 2006). We suggest that most of our larger predators (carabids and cursorial spiders) were not tightly linked to the successfully manipulated isotomid Collembolans, but instead preyed on entomobryid Collembola (Fig. 5.4.a-b). This assumption is supported by the negative correlation between surface-active predator and entomobryid AD in our study, and by an experiment of Bilde et al. (2000) showing the high quality of an entomobryid as prey for a ground-beetle species. In contrast to overall carabid AD, the AD of the most abundant ground beetle species, *L. pillicornis,* was higher with increased availability of isotomid prey. Its increased AD most likely reflects a numerical response, as *L. pillicornis* is a Collembola prey specialist (Sunderland 1975; Hintzpeter and Bauer 1986)

Web-building spiders were more abundant under increased decomposer and herbivore abundance. Feeding preferences of linyphiids for decomposer prey are documented by Agusti et al. (2003), who found that 60% of all sampled web-building spiders (Linyphiidae) from agricultural fields recently had consumed Collembola (mainly isotomids). Weyman and Jepson (1994) and Harwood et al. (2003) documented that web-building spiders in cereals accumulate in areas with increased availability of Collembola and aphid prey. Adults of the three most abundant web-building spider species did not respond to decomposer prey, in contrast immature web-building individuals showed a numerical response to enhanced non-pest prey availability. We therefore suggest a strong feeding link between those small predators and isotomid prey (Fig. 5.4.a). These results and a laboratory study by Marcussen et al. (1999) confirm beneficial effects of aphid and isotomid prey for linyphiid spiders and suggest a strong numerical response of immature web-building spiders in response to increased prey availability. Rove beetles also showed a numerical response to isotomid prey, caused primarily by

individuals from the subfamily Aleocharinae. These small, highly mobile beetles are known to feed on fungi and decaying plants in addition to decomposer prey, with several species being parasitic on Diptera (Walter 1987, Koch 1989, Reddersen 1995). To our best knowledge, predation on aphids has not been recorded for this subfamily; we therefore suggest that the numerical response of this group is not closely correlated to increased aphid numbers (Fig. 5.4.a).

Structural complexity

Conflicting results from studies analyzing the impact of weeds on arthropod communities reflect the complexity of mechanisms affecting generalist predator populations (Norris and Kogan 2005). However, manipulative studies analyzing the impact of habitat structure on generalist predators in order to uncouple links between structure and prey resources in agroecosystems are rare (Sunderland and Samu 2000, Langellotto and Denno 2004). In our study neither surface-active nor vegetation-based generalist predator groups responded positively to increasing vegetation structural complexity. Densities of web-building spiders can be increased by adding structure, as Carter and Rypstra (1995) showed by using wooden crates in soybean fields. Nevertheless, the overall abundance of immature and adult web-builders was not significantly influenced by our structural complexity treatment. In contrast, surface-active spiders and carabids were captured at higher rates in plots with simpler habitat structure.

Lower AD of surface-dwelling predator taxa (spiders and ground beetles) in the structurally more complex treatment suggests that structural characteristics of weedy vegetation may by themselves (i.e. in the absence of indirect effects on prey numbers) negatively affect the density of ground-dwelling generalist predators by altering microclimatic conditions. The most abundant surface active spider (*Erigone* sp.) is known to prefer open and less vegetation-covered patches (e.g. Alderweireldt and Desender 1990), a preference also indicated in this study. Our results suggest that beneficial effects of weeds on generalist predators might be mainly attributed to higher densities of non-pest herbivore prey, which could lead to reduced pest suppression if the predators exhibit a pronounced switch to herbivore prey. This possibility has to be investigated in more detail in order to improve techniques of

conservation biological control, as weeds may either reduce the density and/or change prey preferences of certain generalist predator species, potentially causing reduced pest suppression.

In contrast to overall numbers of web-building spiders, numbers of *T. tenuis* were higher under increased structural complexity. This linyphiid species builds webs at around 10 cm height attached to vegetation and relies on prey captured in webs (Alderweireldt 1994b; Feber et al. 1998; Harwood et al. 2001a). Its higher abundance in the presence of artificial plants can be possibly attributed to enhanced numbers of potential web sites. *Meioneta rurestris*, in contrast, preferred structurally simple plots, reflecting the fact that this species locates its webs on the soil surface (Alderweireldt 1994b, Feber et al. 1998). These species-level effects do not contradict our earlier comments on reduced biocontrol potential through structural complexity, as web-building spider communities in agroecosystems are dominated by immature individuals (Topping and Sunderland 1998).

Analyzing community data at the species level adds significantly to the understanding of predator-prey interactions and predator habitat dependency, a result also supported by Letourneau and Goldstein (2001). Species-specific responses (*T. tenuis* and *L. pillicornis*) would have been masked if only functional or higher taxonomic groups had been analyzed. Although guild and functional group approaches (for discussion see Blondel 2003) may reflect the general response of predators to environmental changes, even in the well-defined functional group of web-building spiders, two taxonomically related species (*T. tenuis* and *M. rurestris*) responded differently to habitat manipulation.

Conclusions

Our results suggest that increased availability of decomposer prey but not greater habitat structural complexity (both of which are often associated with organic farming) enhances densities of generalist predators. However, increased densities of generalist predators did not lead to improved aphid suppression in cereals. The lack of increased control of aphids presumably was due to predators increasing per-capita feeding on increased numbers of decomposer prey. Structural complexity alone did not enhance generalist predator numbers or improve aphid suppression. This result calls into question the assumed positive effect of weeds on improving microclimatic and structural conditions

favorable for generalist predators. Instead, the result supports the hypothesis of beneficial effects of weed-attracted alternative prey and weed-based food (pollen, nectar and seed) for natural enemy populations (Zehnder et al. 2007). As earlier studies in organically managed agroecosystems provide no consistent evidence of improved pest suppression through increased numbers of natural enemies (Letourneau and Goldstein 2001, Östman et al. 2001, Yardim and Edwards 2003), further field experiments investigating the factors that drive prey switching are needed.

Chapter 6 – Cursorial spiders retard aphid population growth at low densities in a winter wheat field in central Germany

6.1. ABSTRACT

Generalist predators contribute to pest suppression in agroecosystems and it is generally assumed that a diverse predator community has a stronger impact on pest numbers. Spider communities are an important component of the generalist predator fauna in arable land, characterized by web-building and non-web-building, cursorial spiders as two distinguishable functional groups. We combined a factorial field experiment that analyzed the impact, separately and together, of equal densities of two spider functional groups (web-builders and non-web-builders) on pest population growth (Aphididae) in wheat, with a molecular approach indicating group-specific aphid consumption rates. Only cursorial spiders retarded aphid population growth in our cage experiment, with no negative impact of web-building spider presence on aphid population growth. This negative effect was only present during the first 5 weeks and disappeared with exponentially growing aphid populations during the last 7 days. The results of a molecular analysis, using aphid specific primers to detect aphid DNA in predator species, indicated a high proportion of aphid consuming individuals among the foliage-dwelling spider species *Xysticus cristatus* (Thomisidae) and the surface-active species *Pardosa palustris* (Lycosidae). Our results on spiders and aphid suppression in wheat suggest that influencing community composition may be more important for improving biological control than fostering predator biodiversity *per se*. Agricultural management practices that specifically support the effective species and functional groups (e.g. mulching for cursorial spiders) should receive considerable attention in modern agricultural farming systems that rely on reduced pesticide use.

6.2. INTRODUCTION

Aphids cause substantial economic loss to farmers in Europe and the US, with estimated annual yield losses ranging from 10 to 250 million US$ in North America (Brewer and Elliott 2004). Generalist predators may contribute to aphid suppression (Symondson et al. 2002), a suggestion supported by negative correlations between pest numbers and predator abundance in field studies (Chambers et al. 1986, Wyss et al. 1995, Östman et al. 2003). This contribution may be fundamentally important in organic farming (Zehnder et al. 2007), as reduced pesticide application promotes generalist predators and potentially strengthens biological control (Thorbek and Bilde 2004, Hole et al. 2005, Schmidt et al. 2005). Aphids colonize crops early in the growing season and occur at low abundance in relatively distinct patches within arable fields (Östman 2002). It has been suggested that generalist predators are most efficient in suppressing aphids during those early stages (Edwards et al. 1979, Chiverton 1986). However, recent experiments provide mixed evidence for effective aphid suppression at low prey densities (von Berg et al. submitted).

Spiders are among the most abundant arthropod predators in temperate agroecosystems (Wise 1993, Nyffeler and Sunderland 2003). Laboratory trials yielded strong evidence for low food quality or even toxicity of aphid prey for spiders (for review see Toft 2005). In contrast, molecular studies, using either antibody or DNA-based techniques to quantify aphid consumption, suggest that web-building (Harwood et al. 2004) and cursorial (Harwood et al. 2005) spiders consume aphids in the field. Reducing generalist predator abundance (including spiders) in field experiments caused higher aphid numbers in some studies (Holland and Thomas 1997a, Lang 2003, Schmidt et al. 2004), but not in others (Holland and Thomas 1997b, Lang et al. 1999).

We combined a factorial field experiment that analyzed the impact, separately and together, of two spider functional groups (web-builders and non-web-builders) on aphid population growth, with a molecular approach indicating group-specific aphid consumption rates. With this combination of approaches we attempted to determine the pest suppression efficiency of each functional group alone and in combination. We hypothesized that (i) web-building and non-web-building spiders are each less effective in suppressing aphid numbers than if combined (assemblage), (ii) spider assemblages prevent

an aphid outbreak from low aphid densities (early colonization stages), and (iii) foliage-dwelling, non-web spiders consume aphids at higher rates than web-builders or ground-active cursorial species.

6.3. MATERIAL AND METHODS

Experimental design

We conducted a 2x2 randomized block experiment (N=9) by establishing 36 closed cages, 3 m apart, in a winter wheat field close to Darmstadt, Germany. Cages were installed March 29, 2006 around 0.7 m² circular areas, located 12 m away from the field edge. Each cage consisted of a 50 cm plastic barrier that was inserted 10 cm in the soil. All cage sides were extended an additional 90 cm with gauze (mesh width < 1 mm) that was stabilized by three upright wooden poles and was closed on top by knotting. The interface between plastic barrier and gauze was sealed with duct tape.

Between April 2 and 17 spiders were removed from the enclosures by means of two pitfall traps without preservative (emptied daily) and six visual searches (6 min search^{-1} cage^{-1}). Other predaceous arthropods trapped by pitfall traps were released daily outside the cages. All removed spiders (N=493) were kept in the laboratory at 20°C, 10 h photoperiod, and were fed two *Drosophila melanogaster* (curly, b.t.b.e. Insektenzucht GmbH, Germany) every two days. On 18 April 24 laboratory-reared, immature aphids (*Sitobion avenae*, Katz Biotech AG, Germany) were introduced into each cage, in two groups of 12 each. Each cage was closed immediately after aphid introduction. One day later spider functional-group treatments were established based on a two factorial design with single functional group treatments (web-builders or cursorial spiders), an assemblage treatment (both functional groups) and a spider- free treatment. Species choice for functional group treatments was based on guild definitions (Uetz et al. 1999) and relative species abundances of spiders removed from the cages. Table 6.1. shows the species frequency within the family/subfamily as estimated from spider removal and the functional group assignment.

Table 6.1. Number of individuals per species in spider functional group treatments. The number of removed individuals per species is given as a proportion (%) of the total number of spiders removed from the same family/subfamily.

			Web-builders		Cursorial		Assemblage	
Species	Family/Subfamily	%	♂	♀	♂	♀	♂	♀
Diplostyla concolor	Linyphiinae	27	1	3	0	0	1	1
Meioneta rurestris	Linyphiinae	20	1	3	0	0	1	1
Erigone sp.	Erigoninae	27	1	2	0	0	1	1
Mangora acalypha	Araneidae	87	0	4	0	0	0	2
Xysticus cristatus	Thomisidae	71	0	0	0	1	0	1
Philodromus aureolus	Philodromidae	100	0	0	0	1	0	1
Pardosa palustris	Lycosidae	62	0	0	4	8	1	3
Pachygnatha degeeri	Tetragnathidae	50	0	0	0	1	0	1

Spiders needed in excess to the ones removed from the cages were captured in the same wheat field. The average number of spiders used for the functional group treatments was estimated from the mean of spiders removed from each cage by using the upper 95% confidence interval (15 individuals) as proxy for high natural spider abundance early in the season ($N \geq 15$ in 17 cages). We established treatments with identical numbers of individuals (including the assemblage) as we focused on the effect of natural spider densities on aphid populations.

After 5 weeks (May 16) we performed a non-destructive estimate of aphid abundance in each enclosure by visually inspecting tillers for 4 minutes per cage. One week later all cages were sampled destructively by aphid tiller counts (12 tillers per cage). After the final tiller count, pitfall traps were reopened and left open for one week to trap surface-active spiders. An estimate of web-building spider abundance was performed by visually sampling all cages two times (2 minutes sampling^{-1} cage^{-1}) during that final week. The number of spiders removed at the end of the experiment provided an estimate of treatment stability over time.

No pesticides were applied to the wheat field in 2006 prior to, or during, the experiment. Average monthly rainfall between April and May 2006 was 72.9 mm with an average air temperature of 12.7°C in Darmstadt (long-term average April-May 1999-2004, rainfall: 46.9 mm, air temperature: 12.5°C).

Molecular analysis

We removed individuals of three spider species by hand searching to avoid contamination with prey DNA. Those spiders were individually stored in cooling boxes (approx. 14°C) and transferred to the laboratory shortly after collection. Ten individuals of representative species within our functional groups were stored at -24°. We analyzed females of the orb-weaver (Araneidae) *Mangora acalypha* (Walckenaer, 1802) as a prominent web-building species, females of the crab spider (Thomisidae) *Xysticus cristatus* (Clerck, 1757) as a foliage-dwelling cursorial spider and females of the wolf spider (Lycosidae) *Pardosa palustris* (Linnaeus, 1758) as a representative surface-dwelling species (references in Bogya 1999, Nyffeler and Breene 1992). We further separately analyzed 10 individuals of *P. palustris* females that carried eggsacs and *P. palustris males* to investigate the hypothesis that adult males and egg-sac-carrying females stop to consume prey. Additionally five individuals of each species were starved for 7 days before freezing at -24°C.

DNA of all spiders including starved controls was extracted using a DNeasy Tissue Kit (QIAGEN), following the manufacturer's instructions with light modifications. After an incubation step at 56°C, 10 µl RNAse A (100µg/µl; QIAGEN) were added to the samples and incubated at room temperature for 5 min. 50µl (*Mangora acalypha*), 70µl (*Pardosa palustris*) and 100µl (*Xysticus cristatus*) were used for further extraction steps, respectively.

The primer pair S102 and A 103 (von Berg et al. submitted) were used to amplify a 316 bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene of *Sitobion avenae*. The PCR was carried out in 10µl, containing 2mM dNTP (fermentas), 1 µM of each primer, 1 µl 10x buffer, 3mM $MgCl_2$, 2.5µg bovine serum albumin (BSA), 0.5 µl DMSO, 1.5 U *Taq* DNA polymerase (invitrogen) and 4,45 µl of DNA extract. Distilled water samples were included in each PCR reaction as a negative control to check for contamination. PCRs were carried out in a master cycler gradient (Eppendorf) with initial denaturation at 94°C for 2 min, followed by 40 cycles of 94°C for 15 s, 63°C for 45 s, 72°C for 45 s, and a final extension step at 72°C for 2 min. PCR products were checked on a agarose gel stained with ethidium bromide. To test the primer pair ability to amplify the DNA of *S. avenae* in presence of predator DNA, we diluted aphid DNA with DNA of the three spiders, respectively, in ratios 1:20.

Data analysis

Treatment stability was analyzed by two-way MANOVA with numbers of web-builders or non-web-builders being sampled from cages at the end of the experimental period as dependent variables and both spider functional groups as fixed factors. Cage-specific linear regression coefficients were calculated based on three dates with known aphid abundance (1st date: aphid introduction, 2nd date: first estimate, 3rd date: second estimate). The regression coefficient is an estimate of the cage-specific aphid population growth. Spider functional group effects were analyzed by performing a two-way ANOVA on the regression coefficients using both spider functional groups as fixed factors. The species/group specific detection rate for aphid DNA was compared between subsets performing a two sample t-test for comparison of proportions. All Analyses were performed using Statistica 7.1 (StatSoft, Germany), means are given with SE.

6.4. RESULTS

We removed an average of 13.7+-0.6 spiders per cage prior to introducing aphids and establishing the functional group treatments. Linyphiids formed 65% of all removed spiders (Linyphiinae 50%, Erigoninae 15%) and only wolf spiders had comparably high densities (18%). All other families were represented by less than 10% of the total number of spiders (Araneidae 6%, Thomisidae 3%, Philodromidae 2%, Tetragnathidae 2% and five other families together with 4%).

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Functional group treatments affected the abundance of cursorial and web-building spiders at the end of the experiment (MANOVA web-builders: $F_{2,31}$=23.53, P<0.001; MANOVA cursorial: $F_{2,31}$=12.18, P<0.001). Removal of one functional group did not affect the abundance of the other group (MANOVA cursorial x web-builders: $F_{2,31}$=1.14, P=0.334). Web-building spiders were 5.3 times more abundant in treatments including web-building spiders (Fig 6.1.; ANOVA: $F_{1,32}$=46.29, P<0.001).

Surface-active spiders were 6 times more abundant in the cursorial spider and assemblage treatment as compared to the web-builder and spider free treatment (ANOVA: $F_{1,32}$=22.79, P<0.001).

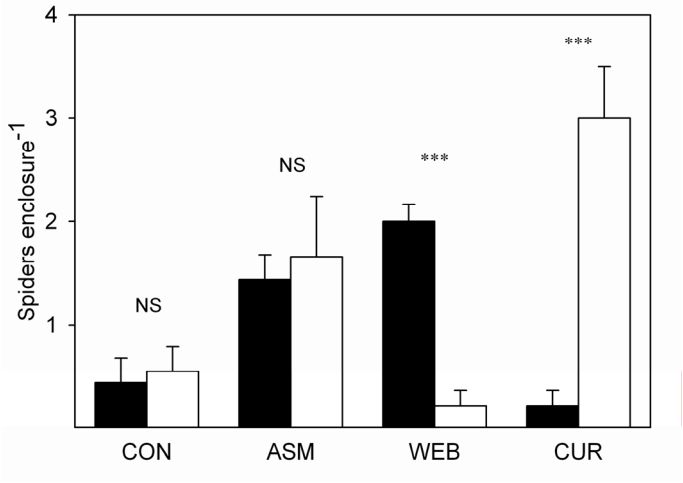

Figure 6.1. Treatment stability in the four spider functional group treatments after the last aphid number estimation (May 23) showing web-building (black) and non-web-building (white) spider abundance in the specific treatments. Treatment abbreviation: CON, spider-free control; ASM, Assemblage (both functional groups); WEB, Web-builders only; CUR, cursorial spiders only. Asterisk denote significant differences; *= P < 0.05;**= P < 0.01;***= P < 0.001 (one-way ANOVA).

Aphid population growth was significantly slowed down in presence of cursorial spiders (Fig. 6.2.; ANOVA: $F_{1,32}$=9.84, P=0.003), with no significant impact of web-building spiders (ANOVA: $F_{1,32}$=0.00, P=0.993).

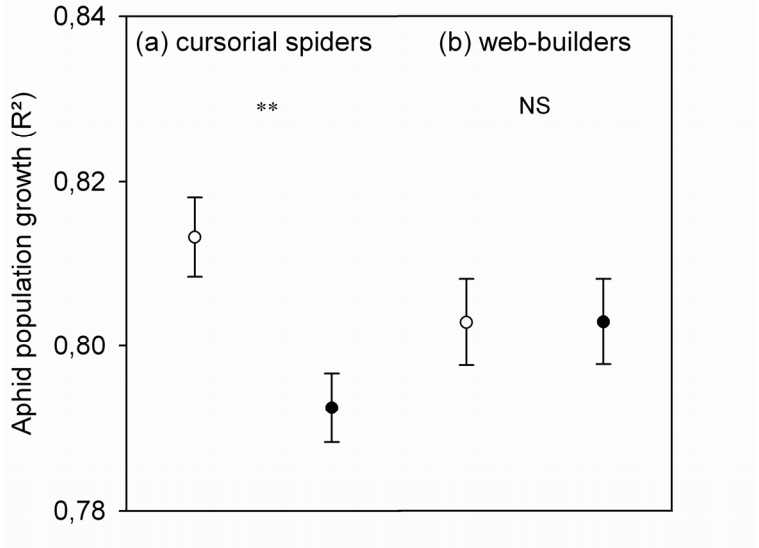

Figure 6.2. Aphid population growth represented by the cage-specific regression coefficient between initial aphid abundance and final aphid density estimates. (a) indicates the impact of cursorial spiders and (b) indicates the impact of web-building spider presence (●) or absence (○). Asterisk denote significant differences; *= P < 0.05;**= P < 0.01;***= P < 0.001 (one-way ANOVA).

Cursorial spiders affected aphids independently of web-building spider presence (ANOVA cursorial x web-builder: $F_{1,32}$=0.02, P=0.887). The negative effect of cursorial spiders was restricted to the aphid population growth during the first 5 weeks (Fig. 6.3.a). Population growth was even higher, although statistically insignificant, in treatments with cursorial spiders during the last week in May (Fig. 6.3.b).

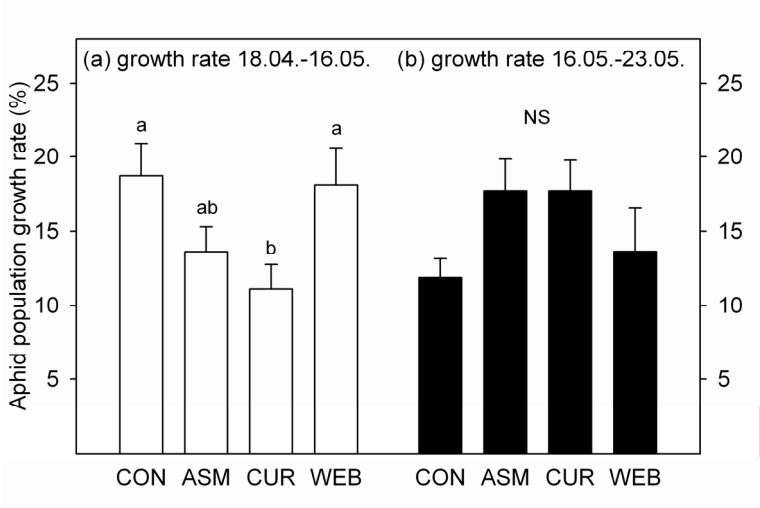

Figure 6.3. Aphid population growth rates between (a) April 18 and May 16 and (b) May 16 and May 23 in different spider functional group treatments. Growth rates are shown as proportional growth between the two dates. Different letters indicate significant differences (LSD post-hoc test). For treatment abbreviations see legend Fig. 6.1.

Xysticus cristatus was the species with the highest proportion of individuals that tested positive for *S. avenae* DNA (Fig. 6.4.).

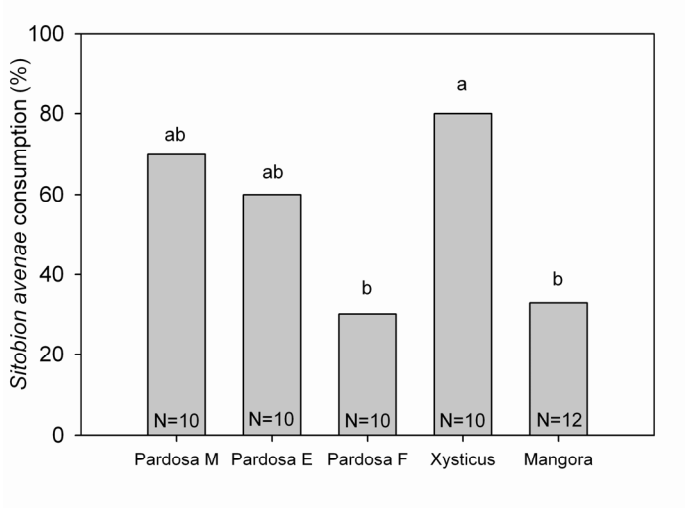

Figure 6.4. Proportion of analyzed individuals per species that tested positive for *Sitobion avenae* DNA with *Pardosa palustris* (M)ales, (E)ggsac carrying females and (F)emales. N indicates the number of individuals tested. Different letters indicate significant differences (two sample t-test for differences between two proportions)

Significantly more individuals of this species contained aphid remains as compared to *M. acalypha* (two sample t-test: t=2.51, df=20, P=0.021) or female *P. palustris* (two sample t-test: t=2.60, df=18, P=0.018). The proportion of positively tested *Pardosa* males tended to be higher than for *M. acalypha* (two sample t-test: t=1.84, df=20, P=0.080). Another trend indicated a higher proportion of individuals containing aphid DNA in *P. palustris* males as compared to females (two sample t-test: t=1.95, df=18, P=0.067). The primer pair showed no amplifications when tested on the three spider species. In presence of predator DNA of all three spiders, amplification of the 316 bp fragment was always successful.

6.5. DISCUSSION

Surface-active spiders slowed-down initial aphid population growth, with no significant effect of web-building spiders on aphid numbers. Holland et al. (1997a&b) suggested that generalist predators may control aphids during early stages of crop colonization when pests occur at low densities. An already established generalist predator population early in the season may therefore be an important prerequisite for successful aphid suppression by natural enemies (Scheu 2001). Our initial aphid density of 24 individuals per m² and the early date within the growing season resemble such suggested optimal conditions for aphid suppression by generalist predators. Our standardized spider densities reflect a realistic estimate of the number of spiders in wheat early in the growing season (Nyffeler and Sunderland 2003). Results therefore support the assumption that cursorial spiders may retard aphid population growth at low densities, but may not prevent an aphid outbreak as isolated component of the natural enemy community (see also Edwards and Sunderland 1979, Chiverton 1986). This significant reduction of aphid population growth through a single spider functional group correlated with times of initial slow population build-up as characteristic for *Sitobion avenae* (Larsson 2005).

The negative impact of this functional group on aphid numbers is remarkable, as generalist predators are often assumed to affect pest populations via synergistic effects only (Symondson et al. 2002). Lang (2003) manipulated overall spider numbers (web-building and cursorial spiders) in experimental plots in wheat and did not identify any significant effect of spider removal on aphid numbers. Spider activity-density was higher in our wheat fields than in Lang's experiment, and cages in his experiment

were not closed. Open cages may allow parasitoids to attack aphids inside cages, a condition that may have contributed to the fact that aphid numbers in Lang's study never reached densities comparable to those in our field experiment. Parasitoids may indeed mask effects of aphid predation by generalist predators as Schmidt et al. (2003) demonstrated that this predator group could be more efficient in aphid suppression than generalist predators.

Web-building spiders consume aphids, with orb-weavers (Araneidae; Wyss et al. 1995) and sheet-web-weavers (Linyphiidae; Sunderland et al. 1986) potentially reducing aphid numbers. Nevertheless, web-building spiders did not affect aphid population growth in our experiment, suggesting limited predation by this functional group. Further evidence is given by the significantly lower proportion of web-building spiders that contained aphid remains as compared to some species in our cursorial spider treatment. *Xysticus cristatus* and *P. palustris* males had the highest proportion of positively tested individuals. *Xysticus cristatus* is an abundant and characteristic species of low growing vegetation and meadows (Roberts 2001) and most hand collected individuals were found on wheat plants sharing a stratum with aphids. Two studies indicate that individuals of this species consume a high proportion of herbivorous prey in hay-meadows (Nyffeler and Breene 1990) and semi-natural grassland (Wegener 1998). Attracting this species to edge areas of arable fields in times before aphids arrive may significantly improve the predator communities' capacity to prevent an aphid outbreak. Male lycosids are generally assumed to reduce feeding activity to a minimum (e.g. Moring and Stewart 1992); nevertheless a substantial proportion of all tested males fed on aphids.

Secondary predation may affect aphid DNA detection rates in generalist predators (Harwood et al. 2001b, Sheppard et al. 2005), as intraguild predation is common between spiders (Wise 2006). Two arguments counteract a strong bias by secondary predation in our analysis. First our sampling for spiders in the end of the experiment reflected our initial, standardized proportions as introduced in our assemblage treatment. Intraguild predation by cursorial spiders on one of both functional groups would have shifted the proportion towards the other group. Secondly cursorial spiders had a significant impact on aphid population growth. A high frequency of intraguild predation would have reduced the number of actively foraging spiders and would have contributed to reduced levels of predation by the remaining spiders.

We conclude that cursorial spiders (e.g. *X. cristatus* and *P. palustris*) may be more important for aphid suppression than web-building spiders (e.g. *M. acalypha*) in early stages of aphid colonization. Management practices that specifically support cursorial species (e.g. mulching, Rypstra et al. 1999) may therefore be of special importance in wheat agroecosystems that rely on conservation biological control.

Chapter 7 - General Discussion

7.1. FARMING SYSTEM EFFECTS

7.1.1. Wheat

The results from the studied long-term experiment (DOK trial) suggest a positive impact of organic fertilization and reduced herbicide application on most below- and aboveground animals in wheat fields. Ecosystem engineers (Lumbricidae), pests (Aphididae), decomposer prey (Diptera larvae) and generalist predators (Araneae) responded as required for improving nutrient cycling and biological control. Some of the results are in line with recent literature reviews on effects of organic farming systems on single fauna components (Bengtsson et al. 2005, Hole et al. 2005). However, the comprehensive study of below- and aboveground biota in the DOK trial offered the unique possibility to analyze the impact of less well studied components of farming systems on community structure. Earlier studies primarily focused on the impact of complex farming systems (Booij and Noorlander 1992), insecticide application (Bogya and Marko 1999), tillage (Thorbek and Bilde 2004) or herbicide application (Bell et al. 2002a) on generalist predators. Fertilization strategy has been shown to directly affect microbial parameters (Dick et al. 1992) and soil animals (Pfotzer and Schuler 1997, Whalen et al. 1998), but studies on the impact of different fertilizer types on generalist predators and their prey are rare (but see Yardim and Edwards 2003).

Animal community composition in the studied wheat agroecosystems differed comparing farming systems that received farmyard manure with those receiving only synthetic fertilizers. Spiders benefited most from organic farming, with enhanced densities under fertilization with manure and absence of herbicide applications. Spider activity-density is known to correlate with vegetation characteristics, with most agrobiont species preferring diverse and densely covered habitats (Rypstra et al. 1999). The numerical response of spiders to organic management in wheat fields was unlikely a consequence of vegetation coverage, as plant coverage was higher under conventional farming. The increased activity-density of web-building and cursorial spiders may rather result from higher prey availability in the organically managed fields. Spiders mirrored the positive response of prey taxa to

organic farming (Diptera larvae); it is known that Diptera form a substantial part of the diet of spiders (Nentwig 1987, Nyffeler 1999). The abundance of another prey taxon (Aphididae) was significantly lower in systems not receiving synthetic fertilizers, a result that partly reflects the known positive correlation between aphids and nitrogen supply (Nevo and Coll 2001, Gurr et al. 2002, Altieri and Nichols 2003, Schütz et al. 2006). Both, the application of inorganic fertilizers as well as reduced generalist predator abundance in the conventional farming systems likely contributed to higher aphid abundance in conventionally managed wheat fields.

7.1.2. Grass-Clover

Spider activity-density and diversity in grass-clover meadows was enhanced through organic fertilization. The organically and conventionally managed farming systems did not receive herbicides (in contrast to the studied wheat fields) and differences therefore solely derived from the application of different fertilizer types. Similar to results from a structurally simpler agroecosystem (wheat, Chapter 2), only spiders responded to farming system, with predatory beetles (Carabidae and Staphylinidae) showing no response to different management strategies. Spiders had a higher activity-density under organic farming early and late in the growing season, with ground-running species responding strongest. Ground-running spiders may feed on pests (Lang 2003, Nyffeler and Sunderland 2003) and a numerical response early in the season could therefore improve biological control. Pests often colonize agroecosystem early in the growing season and established generalist predator populations in times of pest arrival may significantly contribute to herbivore control (Scheu 2001). Data suggests a strong impact of vegetation coverage on spider activity-density late in the season (October), but vegetation characteristics did not correlate with spider activity-density in April. Fertilization with manure is known to enhance decomposer animal abundance (Pfotzer and Schuler 1997) and may therefore affect predators that are linked to prey from the belowground subsystem. Synthetic fertilizers, as applied to conventional grass-clover plots in the DOK trial, may detrimentally affect soil animals (Bulluck et al. 2002). The positive numerical response of spiders in organically managed grass-clover plots may be caused by higher prey availability in organically managed fields early in the season and by higher plant cover later in the season.

Experimentally reduced densities of the most abundant ground-running spider genus (*Pardosa*) did not enhance herbivore or decomposer abundance. In contrast to potential prey, other spider guilds benefited from *Pardosa* removal. Ground-running spiders (excluding *Pardosa*) and foliage running spiders had significantly higher activity-densities in plots with reduced *Pardosa* density. Those results indicate intraguild interactions to affect spider communities in arable land. Wolf spiders feed on pests (e.g. aphids; Madsen et al. 2004, Harwood et al. 2005) and the positive numerical response of non-manipulated spider species to *Pardosa* removal potentially masked effects on herbivore or decomposer prey abundance. Herbivore densities in the studied grass-clover system were presumably not enhanced through *Pardosa* removal due to compensatory predation of other spider species in absence of *Pardosa*.

7.2. FACTORS REGULATING GENERALIST PREDATORS

Spatial patterns of pest prey individuals and the degree of association with predators affects the capacity of natural enemies to control herbivores (Bommarco et al. 2007). The spatial pattern of web-building spiders did not resemble the distribution of available pest prey (Aphididae) in alfalfa fields. In contrast to aggregation in response to prey clusters, web-owners in alfalfa had significantly fewer neighbors close to their own webs than expected under a random distribution. This spatial pattern was restricted to periods of maximum spider activity density (web-builders and ground-runners), therefore intraguild interactions (competition or intraguild predation) likely contributed to the development of the observed pattern. Alfalfa fields resemble structurally complex agroecosystems such as grass-clover meadows in the DOK trial. Web-building spider association to aphid prey is documented in structurally simpler agroecosystems (winter wheat; Harwood et al. 2001a, 2003) suggesting that increased habitat complexity may weaken the spatial association between predators and prey. This suggestion is supported by results for ground-active generalist predators and their prey in alfalfa (Pearce and Zalucki 2006). Indications of intraguild interactions in alfalfa agroecosystems in Kentucky support findings from grass-clover meadows in Switzerland and both studies suggest intraguild interactions to contribute to spider abundance, community composition and spatial distribution in structurally diverse agroecosystems.

Experimentally enhanced abundance of alternative prey from the decomposer subsystem caused a numerical response of web-building spiders and rove beetles (Staphylinidae) in wheat. Two surface-hunting generalist predator taxa (Carabidae and Lycosidae) did not respond to enhanced prey levels. Pest prey (Aphididae) mirrored the response of decomposer prey, being significantly more abundant in enhanced non-pest prey treatments. Such positive prey-prey interactions (Holt 1977) may reduce herbivore suppression by generalist predators, as alternative non-pest prey may distract predators from feeding on "target" pest prey. Organic farming practices, such as low-tillage or organic fertilization, enhance decomposer densities (Hole et al. 2005). However, results from the present field experiments suggest that pest suppression is not necessarily improved. Results further indicate that increasing habitat complexity alone might not improve herbivore suppression in wheat. Weedier arable fields in organically managed agroecosystems increase the structural complexity, attract additional prey and supply certain generalist predator groups (ground and rove beetles) with supplementary food sources (pollen, nectar and seeds; Norris and Kogan 2005). The last two characteristics of weeds may affect generalist predators similar to enhanced non-pest prey availability by distracting predators from feeding on pest species. Results of this study suggest that structural complexity alone may not necessarily enhance predator abundance, with some ground-active taxa (spiders and ground beetle) even preferring less complex habitats. Generalist predators often benefit from weeds in arable fields (Moreby et al. 1994), results of this study suggest that this numerical response is mainly caused by an additional supply with weed-related food resources (supplementary food sources or alternative herbivore prey). The positive numerical response of generalist predators to weeds therefore does not necessarily improve pest suppression.

7.3. IMPLICATIONS FOR BIOLOGICAL CONTROL

Surface-active spiders were able to slow-down aphid population build-up from low initial densities up to three weeks after aphid colonization. Web-building spiders and an assemblage of both spider functional groups did not affect aphid numbers, even if compared to predator free control cages. Aphid populations grow exponentially, a characteristic that is reflected by threshold based decisions about insecticide spraying in arable land (Larsson 2005). Spiders had no impact on aphid numbers after the

initial population growth period, with aphid populations reaching pest status in all spider functional group treatments (based on central European thresholds; Larsson 2005). This study suggests that functional group composition of generalist predators does matter for biological control and that functional group diversity is not necessarily improving pest suppression if the frequency of an aphid-consuming functional group is reduced in favor of a less effective generalist predator group. Negative effects of predator diversity may further be enhanced by intraguild predation (Finke and Denno 2005). Specialized predators are introduced or specifically targeted by certain management practices (Pickett and Bugg 1998, Hajek 2004), but generalist predator enhancement *per se* may even reduce biological control if it is associated with increased levels of intraguild interactions or enhanced alternative non-pest prey levels.

7.4. PROSPECTS

Several experimental and molecular studies indicate consumption of aphid prey by spiders (Wyss et al. 1995, Greenstone and Shufran 2003, Harwood et al. 2005), carabids (Kielty et al. 1999, Lang et al. 2003) and staphylinids (Kyneb and Toft 2004). In contrast, other studies suggest weak herbivore suppression by generalist predators (Holland et al. 1996, Holland and Thomas 1997a, 1997b, Lang et al. 1999). The present studies demonstrate the complex interactions between predators, prey and their environment. Intraguild interactions (cannibalism, competition or IGP) are certainly among the most important biotic factors that affect generalist predator communities and their role in biological control. Ecological research in arable land has significantly contributed to a change of the dogmatic view that pest suppression is an ecosystem service exclusively provided by specialists. Integrated solutions to optimize herbivore suppression today target generalist predators and parasitoids, but the impact of certain agricultural practices (e.g. pesticide application, tillage) on predator communities has received considerable more attention than others (e.g. fertilization, crop rotation). Effects of agricultural management on generalist predators are increasingly understood, but more information is needed about the ultimate factors and mechanisms that act on generalist predators in organically managed arable land. Results indicate that alternative non-pest prey only enhances biological control if decomposer prey levels decrease in times of increasing pest abundance or if predators actively switch

from non-pest to pest prey in a density independent manner. The results further document the need for experiments that identify predator specific feeding links to pest prey in agroecosystems, as management practices that foster generalist predator communities *per se* may not improve pest control. Understanding factors that affect prey switching between pest and non-pest prey should be a major topic in future research, as deeper insights may directly contribute to improved biological control in organic farming systems.

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Acknowledgements

I am deeply grateful to Stefan Scheu for the support and guidance during this PhD, it was and will always be a pleasure to work with you. The same is true for my co-supervisor David H. Wise, I enjoyed every second in Lexington and discussions with you are always an amazing source for new approaches and ideas.

Thanks to Uli Brose, Prof. Dr. Ralf A.W. Galuske and Prof. Dr. Barbara Drossel for accepting to take part as examinators for my PhD dissertation.

Financial support by the German Science Foundation is gratefully acknowledged

The AG Scheu was a cosy home for the last 3 years and I thank all members for the fantastic work environment. Discussions with Karsten von Berg contributed significantly to this unique atmosphere ("Keimzelle Generalistische Prädatoren"). Mark Maraun always answered my sometimes clumsy questions with great patience. Project students and collaborators like Bernhard Klarner, Dora Volovei, Michael Bonkowski, Britta Merkel, Olivera Vučić-Pestić, Dominique Haubert and Liliane Ruess further made this project an enjoyable experience.

I am thankful to the CONSIDER network, as the experienced members showed great patience with a young scientist. Andreas Fließbach and Paul Mäder provided the possibility to work at the DOK trial, many thanks for this amazing possibility. Yael D. Lubin and Efrat Gavish made the fascinating stay in Israel very enjoyable, thanks for this wonderful time. Werner Jossi and Carsten Thies provided valuable information or possibilities to work in Switzerland and Göttingen.

Kerstin Endlweber deserves special thanks as she tolerated every field trip, research stay and hectic moment during this PhD. More than once she even became part of it, I am deeply grateful for your support.

The fantastic relationship to my parents and their always supporting presence made my way of life possible. To them as well as to my brother Ben I am everlasting thankful, even though we were not always on the same page.

Ein besonderes Dankeschön möchte ich an meinen Opa richten: Während der Studienjahre hattest du immer ein offenes Ohr und hast damit ganz wesentlich zum erfolgreichen Abschluss meines Studiums beigetragen. Vielen Dank!

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Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbstständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Die Auswertung der Proben zur Bodenchemie, Mikrobiologie, Nematoden, Protozoen und Enchytraeiden Abundanz in Kapitel 2 wurden nicht von mir durchgeführt, Ergebnisse stammen von meinen Koautoren.

Ich habe noch keinen Promotionsversuch unternommen.

Darmstadt, den 11. April 2007

Klaus Birkhofer